

THE SYSTEMATICS, DISTRIBUTION, AND ZOOGEOGRAPHY OF THE MARINE HATCHETFISHES (FAMILY STERNOPTYCHIDAE)

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TABLE OF CONTENTS

Introduction	2
Methods	3
Osteological Character Complexes	7
Osteological Conclusions	15
The Fossil Record	22
Systematics	29
Family Sternoptychidae	29
Key to the genera of Sternoptychidae	29
Genus <i>Argyropelecus</i>	31
Key to the species of <i>Argyropelecus</i>	32
<i>Argyropelecus affinis</i>	34
<i>Argyropelecus gigas</i>	38
<i>Argyropelecus hemigymnus</i>	42
<i>Argyropelecus aculeatus</i>	48
<i>Argyropelecus olfersi</i>	52
<i>Argyropelecus sladeni</i>	56
<i>Argyropelecus lynchus</i>	63
Genus <i>Sternoptyx</i>	67
Key to the species of <i>Sternoptyx</i>	68
<i>Sternoptyx obscura</i>	69
<i>Sternoptyx pseudobscura</i>	72
<i>Sternoptyx diaphana</i>	75
Genus <i>Polyipnus</i>	79
Key to the species of <i>Polyipnus</i>	82
<i>Polyipnus tridentifer</i>	86
<i>Polyipnus sterope</i>	88
<i>Polyipnus spinosus</i>	89
<i>Polyipnus oluolus</i>	90
<i>Polyipnus indicus</i>	91
<i>Polyipnus nuttingi</i>	92
<i>Polyipnus laternatus</i>	92
<i>Polyipnus omphus</i>	94
<i>Polyipnus aquavitus</i>	96
<i>Polyipnus unispinus</i>	97
<i>Polyipnus triphanos</i>	97

<i>Polyipnus polli</i>	98
<i>Polyipnus asteroides</i>	99
<i>Polyipnus matsubarae</i>	101
<i>Polyipnus ruggeri</i>	102
<i>Polyipnus kiwiensis</i>	103
<i>Polyipnus metcori</i>	104
Discussion and Conclusions	104
Patterns of Distribution	104
Geographic Variation	106
Distributional Factors	107
Zoogeographic Regions	110
Acknowledgments	114
Summary	115
Appendix A	115
Appendix B	117
Literature Cited	123

ABSTRACT

The systematic history of the Sternoptychidae has been one of instability in higher classification. A study of comparative osteology indicates that the hatchetfishes are closely related to the Gonostomatidae but differ from them in certain significant aspects. The Sternoptychidae are therefore given familial rank.

Fossil evidence indicates that the family probably arose during the early Tertiary and reached its present evolutionary grade by the middle Miocene. Three phylogenetically divergent genera are recognized, these being *Argyropelecus*, *Polyipnus*, and *Sternoptyx*, with seven, seventeen, and three species respectively. Many species exhibit geographical variation and morphologically distinct populations were defined in some instances.

The genera differ broadly in habitat as well as morphology. *Argyropelecus* is a high seas pelagic genus limited to the upper 600 m. *Sternoptyx* shows a similar pattern horizontally but inhabits the 500 to 1500 m depth zone. *Polyipnus* occurs only in close association with land, exhibiting a distribution and speciation pattern similar to many tropical shore species. *Argyropelecus* and *Sternoptyx* spe-

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cies are seemingly restricted to waters with similar hydrographic and biological properties. Certain species assemblages are used to define zoogeographically distinct areas of the world's oceans.

INTRODUCTION

The systematic history of marine hatchetfishes begins with Hermann's (1781) description of a photophore-bearing fish he called *Sternoptyx diaphana* (from the Greek words "sternon" (chest) and "ptyx" (plate)) and from which the family derives its name. Hermann called attention to the extraordinarily deep and compressed body shape and thus established one of the principal descriptive characteristics of the group. The genus *Argyropelecus* was described by Cocco in 1829 and both genera then appeared in the classic work of Cuvier and Valenciennes (1849).

Günther (1864: 384) placed the above genera in the family Sternoptychidae and included also other midwater genera (presently placed in the family Gonostomatidae) using such characteristics as photophores and gill structures. In addition, *Argyropelecus* and *Sternoptyx* were given subfamilial rank characterized by the presence of a spinous dorsal blade.

Gill (1884), while recognizing that the congener of the Gonostomatine fishes was allied to the Sternoptychidae, nevertheless restricted the family to include only *Sternoptyx* and *Argyropelecus*. He recognized too, a degree of difference between these genera and gave them subfamilial rank.

Günther (1887) added the newly described genus *Polyipnus* to his family Sternoptychidae, which still included the present gonostomatid genera. Goode and Bean (1896) followed Gill in recognizing three families from Günther's one: Gonostomatidae, Maurolicidae, and Sternoptychidae; and in addition, placed the genus *Polyipnus* with the Sternoptychidae. Garman (1899), citing the similarity of the larval forms of Goode and Bean's three

families, returned to Günther's original scheme. Brauer (1906: 101) later continued to recognize Günther's classification.

Regan (1923) attempted to clarify the earlier confusion by examining osteological characters, thereby giving more explicit definitions to the taxa. This resulted in assignment of the genera *Sternoptyx*, *Argyropelecus*, and *Polyipnus* to the family Sternoptychidae, while other related genera were placed in the family Gonostomatidae. Such basic differences as the absence of a basi- and alisphenoid bone in the former family were cited as justification for this split. Regan's classification was later accepted by Norman (1930, 1944) and Berg (1940).

Regan's work did not resolve the problem of family relationship and taxon rank, however. While generally recognizing Regan's classification, Fowler (1936) gave the Maurolicidae familial rank and further complicated the issue by including the genus *Valenciennellus* with Regan's Sternoptychidae. Gregory and Conrad (1936) included *Maurolicus* in the family Sternoptychidae, acknowledging the primitiveness of this genus, as well as its role as a possible congener of Regan's Sternoptychidae. They cited the deep, compressed body form as an evolutionary trend in the family. Smith (1953) essentially returned to Goode and Bean's old classification while Hubbs (1953), referring to the connecting links in the evolution of the Sternoptychidae from the Gonostomatidae, recommended a revival of Günther's classification, thus reducing Regan's Sternoptychidae to subfamilial rank. While Rehnitz and Böhlke (1958) and Ebeling (1962) have accepted Hubbs' proposal, most modern authors recognize Regan's classification (Schultz, 1961; Morrow, 1964; Backus et al., 1965; Berry and Perkins, 1965). However, Greenwood et al. (1966) indicate that the Sternoptychidae are a specialized offshoot of the Gonostomatidae and, although still recognizing the former as a separate family, they

suspect that further morphological study will support the earlier conclusions of Hubbs.

Historically then, there has been a failure to achieve a stable classification of the Sternoptychidae. The numerous reasons for this failure may be attributed primarily to the use of superficial or highly variable character complexes, the lack of detailed morphological studies using osteological or other acceptable criteria, and subjective conceptual differences concerning the family rank.

The first consideration of a systematic study of the Sternoptychidae must include an attempt to clarify some of the historical confusion. Accordingly, a comparative study of primarily osteological character complexes was undertaken with the following objectives: to help elucidate the family question; to provide characters for explicit definitions of the taxa; and to comment on generic relationships and evolutionary trends among the genera and species complexes. The character complexes cited were sufficiently numerous and functionally distinct to reasonably satisfy the initial objectives. The gonostomatid genera *Maurolicus* and *Valenciennellus* were chosen for comparison with the Sternoptychidae as they are thought, classically, to be most closely related to them, and because any other choice would have to involve a detailed study of the Gonostomatidae.

The use of osteological characters and character complexes as the primary criteria in a systematic study involves the following concepts: 1) The skeletal system is a major constituent of the functional morphology of an individual and should reflect its general evolutionary history. 2) As selection acts on a particular morphological region, it alters the osteology of that region. Both between and within regions, osteological characters may be independent with regard to rate and direction of evolution. 3) The skeletal system is not strictly a single one with a limited function and morphology. Rather, it may be thought of

as a series of semi-independent systems or "functional units," each reflecting the functional requirements of that particular unit. 4) An osteological study results in a composite of individual character complexes, some of which may be primitive, others advanced, but which reflect the evolution and specialization within phyletic lines. 5) Osteological characters have been shown to be as consistent as other characters in reflecting phylogeny and evolution. We know more about osteology and its limitations. 6) Paleontological evidence is primarily osteological.

Fossil evidence was also considered and a detailed study was made of the fossil record to provide additional information on the evolutionary history and relationships ascertained from the osteological results. After using these in resolving the family question and in presenting an evolutionary history, the various higher taxa were defined and a revision of the respective genera undertaken.

The widespread occurrence and ease of capture of the Sternoptychidae make them ideally suited for studies involving population structure, speciation, and distribution in the midwater or mesopelagic environment. Several recent studies (Haffner, 1952; Ebeling, 1962; Nafpaktitis, 1968) have indicated some of the distributional patterns of certain midwater fishes and the possible factors involved therein. This study attempts to examine some of these factors with regard to present sternoptychid distributions.

METHODS

Material. Because of the vast amount of material examined a detailed list of specimens and stations is not included in this work. Appendix A lists the institutions, vessels, and respective cruises from which material was obtained. A detailed listing of material examined is on permanent file in the Museum of Comparative Zoology, Harvard University.

Collecting and sampling techniques. In a study such as this one, involving material from so many cruises employing a wide variety of gear and using various fishing philosophies, the sources of sampling bias are too numerous to list. However, some of the major problems can be discussed.

Horizontally, there is a marked difference in the amount of sampling between areas. A few areas have been adequately sampled (California, North Atlantic) while others have not been sampled at all. The Pacific in general, the South Atlantic, and the Indian Ocean—especially the southern and eastern portion—are markedly under-sampled. The “pseudopelagic” or near-shore midwater environment has not been sampled in most parts of the world. In most cases sampling was seldom extensive enough to appreciate any micro-distributional features or seasonal variation (see Pearcy, 1964).

In addition to differences in collecting gear, there were significant differences in fishing philosophy. Some cruises were faunal surveys with many oblique tows to numerous depths. Other cruises were interested in sampling only over a certain depth range (e. g., upper 500 m), while still others sampled particular environments or collected in sound-scattering layers. The majority of cruises were diurnally biased, collecting primarily in the upper 200 m at night and much deeper during the day. The upper 500 m was much more extensively sampled than deeper waters, especially at depths below 1000 m.

A wide variety of fishing gear was employed. The gear most frequently used was the 10' Isaacs-Kidd midwater trawl. Many other types of trawls, ring nets, plankton tows, and even dip nets, provided material. Depth determination and data recording varied widely. For example, it was often impossible to tell if a certain sample was a horizontal or oblique tow, or whether the depth recorded was calculated by triangulation or determined electronically with automatic depth recorders.

There is an abundance of literature on the problems encountered in sampling mid-water organisms from behavioral responses to gear characteristics and performance. For a comprehensive discussion of the problem see Suzuki (1961), Aron (1962), and Harrison (1967).

Hatchetfishes are easily caught by slow moving towed nets. There is some correlation between size of tow and size of individuals taken. Plankton tows take primarily very small individuals, while 10' Isaacs-Kidd trawls take larger specimens. In general the 10' IKMT appears to under-sample the large individuals, although it does on occasion catch the very largest individuals of a species. Comparisons with catches by the huge Engalls trawl in the northeast Atlantic show that there are more of the larger individuals present than IKMT samples indicate. In the case of *Argyropelecus gigas*, the largest specimens ever recorded were taken in numbers by this trawl. With the exception of *Argyropelecus gigas*, hatchetfishes are small sized and are adequately sampled, except for the largest sizes, by the standard IKMT. Indications are that more work with large midwater trawls, especially those that operate at depths greater than 500 m, will add a new dimension to the “lilliputian” midwater fauna (see Harrison, 1967: 104).

Measurements and counts. The methods of measurement usually used were those described by Hubbs and Lagler (1947: 13), although the peculiar morphology of the Sternoptychidae necessitated several adjustments. In addition, measurements were adjusted so that in some cases reference points are somewhat different between the genera. Measurements of standard length (SL) and body depth (BD) were made with needle point dividers to the nearest whole millimeter. Other measurements were taken with vernier calipers, and were determined to the nearest tenth of one millimeter.

Characters chosen for measurement were those which appeared to have systematic

importance, or could be directly or indirectly tied to ecological considerations. The following measurements were taken: Standard length—measured from the end of the snout to the farthest extension of the well-marked caudal peduncle (in *Sternoptyx* the peduncle asymmetrical, the lower lobe extends farthest posteriorly). Body depth—in *Argyropelecus* and *Polyipnus* measured from the origin of the dorsal blade to the most ventral extension of body margin, excluding ventral keel scales; in *Sternoptyx* measured from the end of the dorsal fin and essentially a trunk measurement. Dorsal blade—height measured from dorsal body margin to greatest extension of major element in the blade along blade axis (in *Sternoptyx* there is only one element). Jaw length—measured from the point of the retroarticular to the anteriormost extension of the lower jaw. Jaw width—measured in the lateral plane between the left and right lower jaw articulations. Caudal peduncle—a depth measurement across the narrowest dorsal-ventral axis of the caudal peduncle. Abdominal length—used only in *Sternoptyx*, measured from the dorsalmost point of the supra-anal photophore to the posteriormost extension of the caudal peduncle. Supra-abdominal photophore—a *Sternoptyx* character measured from the dorsalmost point of the supra-anal photophore to the dorsal body margin normal to the midabdominal axis. Dorsal fin length—in *Sternoptyx* measured from the origin of the anteriormost fin ray to the origin of the posteriormost fin ray. Orbital diameter—in *Polyipnus* measured along the anterior-posterior axis. Post-temporal spine length—in *Polyipnus* measured from the ventral origin of the spine to its tip. Head length—in *Polyipnus* measured from the end of the snout to the posterior opercular margin. Photophore measurements—measured from the farthest extension of the dark pigmented photophore margins.

The following counts were made. Gill raker number: the number of gill rakers

on the first branchial arch of the left side; only clearly defined rakers were counted. Caudal, median, and pectoral ray counts were as per Hubbs and Lagler (1947). Vertebral counts were made from fossils, X-ray photographs, or cleared and stained specimens. Vertebral counts included all separate vertebrae, except the urostylar element(s); vertebral counts for fossil material included only those elements posterior to the major element in the dorsal blade.

Keys and key characters. Because of the damaged condition of many specimens in midwater collections, keys include several characters to aid in identification. Care must be taken when making measurements on, or using key characters with, damaged specimens. Keys were constructed for adults and late juveniles only, and are roughly limited to individuals greater than 20–25 mm in standard length. Photophore complement, especially in the anal series of *Polyipnus*, is complete only in the adults. Most of the key characters are discussed in the descriptions; however, several of the more common ones are expanded as follows. The post-temporal spine in certain species of *Polyipnus* bears small basal spines on its ventral-lateral surface; dorsal, postabdominal, and preopercular spines are often worn or broken, especially in larger individuals. Subcaudal spines appear late in ontogeny and are always small. Spinose borders of the preopercle and ventral keel scales are obvious and well developed. Canine teeth may be missing or broken, but when present they are conspicuously longer than other teeth. Teeth present on the midline of the posterior vomerine shaft in certain species of *Polyipnus* are difficult to see in small specimens. Caudal ray pigment is often reduced by loss or abrasion of the caudal fin. Pigment characteristics used are dark melanistic areas which appear stable in most common preservatives if the specimens are undamaged. Preopercle spine characteristics in the *Argyropelecus lychnus* complex

are sometimes variable, and occasionally borderline cases occur. While keys were constructed for individual identification, population and distribution data should always be checked.

Photophores (Figs. 17 and 18). Photophore nomenclature was adopted from Schultz (1961). The photophore groups are as follows: preorbital (PO)—a single photophore located anterior to the eye (ventrally located in *Sternoptyx*); postorbital (PTO)—a single photophore just posterior to the eye; preopercular (PRO)—a single large photophore located at the ventral margin of the opercular region; subopercular (SO)—a single small photophore at the posterior ventral margin of the opercular region; suprapectoral (SP)—a series of three photophores (two in *Argyropelecus*) in the region above the pectoral fin; branchiostegal (BR)—a cluster or group of photophores located in the branchial region; isthmus (I)—a group of five to six photophores along the anterior ventral body margin below the preopercular complex; abdominal (AB)—a large group of 10–12 photophores along the ventral abdominal body margin; preanal (PAN)—a group of three to five photophores located in the region just above and posterior to the pelvic fins; anal (AN)—a variably numbered group of photophores located along the ventral body margin in the region of the anal fin; subcaudal (SC)—a group of four photophores along the ventral body margin in the region of the caudal peduncle; these usually form a single close-packed cluster but may be separated in certain species of *Argyropelecus*; supra-abdominal (SAB)—(absent in *Sternoptyx*) a series of three (*Polyipnus*) or six (*Argyropelecus*) photophores above the abdominal series along the lateral body margin; supra-anal (SAN)—(absent in *Argyropelecus*) a single photophore in *Sternoptyx* which is anterior to and raised above the anal group; a series of three photophores in *Polyipnus* anterior to and usually raised above the anal group; in

certain species the three supra-anal photophores are anterior to but are essentially continuous with the anal series; lateral (L)—a single photophore in the midlateral region of the trunk found only in *Polyipnus*.

Photophore number and position are remarkably constant in the Sternoptychidae. However, rare individuals do have photophores in somewhat abnormal positions or occur with an abnormal number in any group. The number is constant in most photophore groups throughout a genus, although the resultant pattern may be somewhat different owing to differences in body form or photophore location. No sexual dimorphism in photophore number or pattern was observed.

Clearing and staining. For the osteological study, a series of specimens of each species examined was cleared and stained using a slightly modified trypsin digestion technique described by Taylor (1967). This method gave excellent results even on specimens preserved for long periods of time. In addition, the method is considerably more rapid than other techniques. Distorted specimens often gave good results since they were partially relaxed by the digestion process.

Analysis and presentation of data. Because of the magnitude of material examined, computer techniques were employed extensively. Programs (primarily in the Fortran IV language for use with the IBM 7094 at the Harvard University Computation Center) were designed to plot and analyze the data. Four types of data cards were punched and then cross-indexed by cruise and station number. One card contained station location and depth plus hydrographic and time data where available. The catch card incorporated the total catch, the size breakdown of the catch, and other data such as maximum size or size of gravid females. Morphometric and meristic data cards completed the raw data input.

Horizontal distributions were computer

plotted and broken down into three arbitrary, relative abundance categories which were indicated by separate symbols. These plots formed the basis for the distributional charts on each species. Plots of juveniles and gravid females did not differ significantly from overall plots, so they were not included in the data presented.

Depth data were subjected to two separate analyses. The first was a tabular breakdown of all depth data taken primarily by IKMT and in which depth was determined by pressure depth recorders in most cases. Depth figures represent only maximum net depths and in many instances probably represent oblique tows, although where this was definitely indicated oblique tows were excluded. The results are listed in Appendix B. This method was particularly helpful in appreciating sampling bias. For the second analysis, only known horizontal tows were used and a plot of the rate of catch in fish-per-hour against depth was made. Only rates greater than one fish/hour (one-half fish/hour in certain species) were plotted. A much finer definition of the depth range of each species was thus obtained, although the sampling bias cannot be fully ascertained.

Where hydrographic data were available, temperature-salinity plots were made for each species and compared with known water mass T-S envelopes. These plots formed part of the data for Table 24.

Morphometric and meristic data were analyzed using standard statistical methods. All proportional data were computer plotted against standard length, and regression statistics were computed by the least square method. Only adults or late juveniles were used, and relationships were linear in all cases. Variability was quite low in most instances, and as long as stratified samples were taken (covering most of the length range of a species), excellent repeatable regression lines were obtained. Confidence limits decreased with sample size to about 20 individuals, beyond

which little reduction could be obtained. Stratified samples as small as eight individuals were adequate to establish good regression lines, which were consistent with larger samples in most cases. In many areas, sample sizes were inadequate and the population parameters presented must be verified further with more sampling. Slope differences were tested statistically and are presented in the various tables. Positional differences between populations could often be detected although the slopes were not statistically different. These, when noted, were plotted (Fig. 23). Meristic data were plotted and a difference of two standard errors on either side of the mean formed the basis for statistical comparison. Dorsal blade height in *Argyrolepecus hemigymnus* was plotted in the same manner as meristic data. The slope of blade height to standard length was very low (.008-.02), so that comparisons between individuals over a small length range (22-28 mm) were considered equivalent.

Oceanographic data were obtained from various standard sources (Fuglister, 1960; Sverdrup et al., 1960; Muromtsev, 1963; Schroeder, 1963) and from cruise reports.

OSTEOLOGICAL CHARACTER COMPLEXES

Caudal skeleton (Fig. 1). There is a definite similarity among the caudal skeletons examined. Features in common include: somewhat flattened neural and haemal spines; three characteristic hypural or hypural-like elements in the ventral caudal lobe (definitions and abbreviations of bones follow Norden (1961); see Weitzman (1967a) concerning definition of a hypural element); often one or more post-terminal vertebrae; one or two free epurals (except *Sternoptyx*); and a caudal fin ray count of $10 + 9$, with a varying number of dorsal and ventral procurent rays.

There is considerable variation in the degree of fusion of hypural elements. With the exception of the *Argyrolepecus affinis* and *Polyipnus spinosus* species complexes,

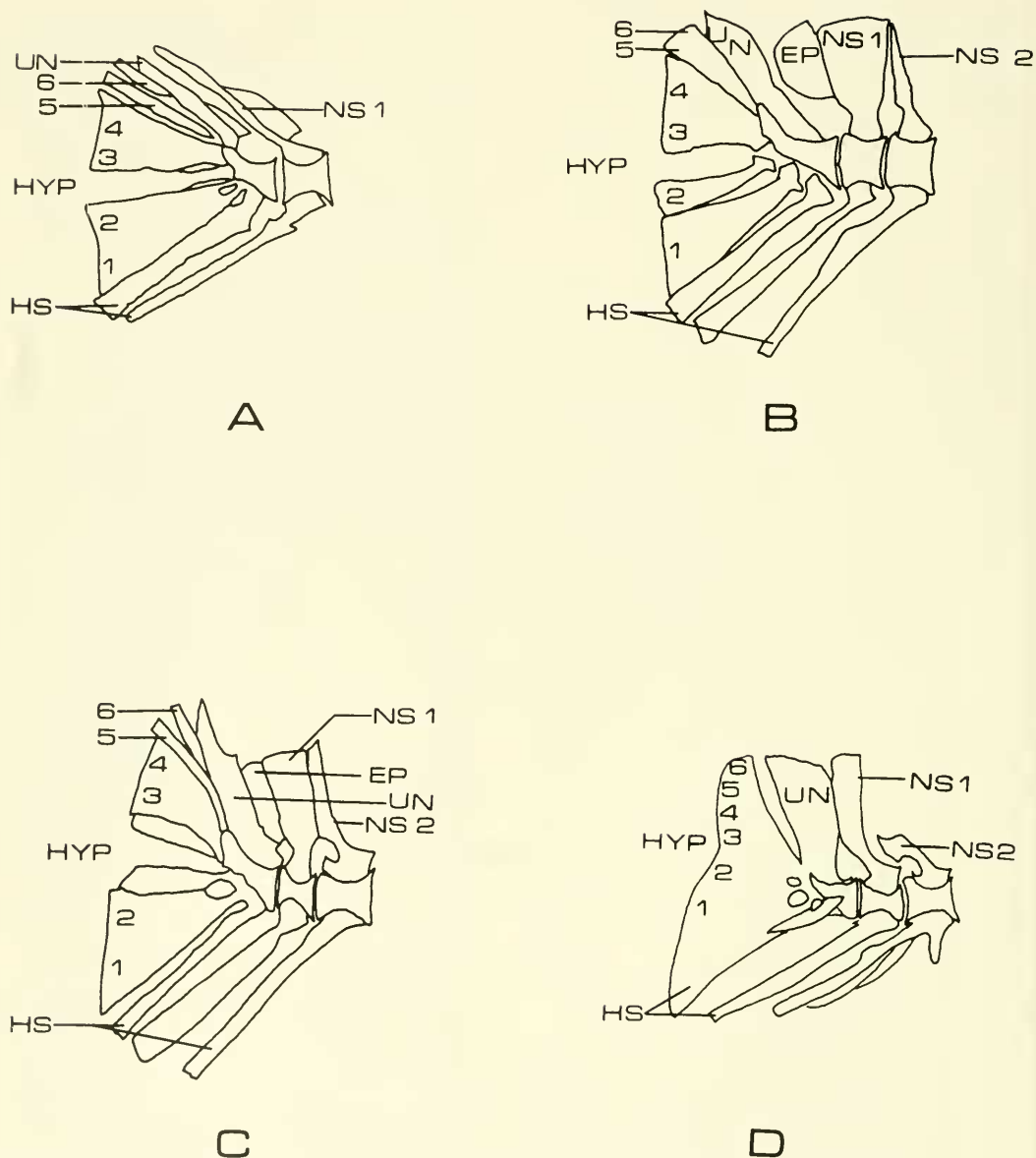


Figure 1. Caudal Skeleton: A. *Maurilicus muelleri*; B. *Argyropelecus affinis*; C. *Polyipnus asteroides*; D. *Sternoptyx pseudobscura*. Abbreviations: EP = epural; HS = haemal spine; HYP = hypurals; NS = neural spines; and UN = uraneural.

hypurals 1-2 and 3-4 are always fused. In some cases, there is complete (*Sternoptyx*) or almost complete (*Valenciennellus*) fusion of hypural elements.

The following are the important evo-

lutionary features. The caudal skeleton of *Maurilicus* appears primitive and is similar to the caudal skeleton of *Vinciguerria* as illustrated by Weitzman (1967b). The three sternoptychid genera are character-

ized by a modification of the first neural spine into a short triangulate, vertical blade. The second neural spine often supports the first. In marked contrast, the gonostomatid genera examined (also *Vinciguerria*, see Weitzman, 1967b) show little modification in this area, and the first neural spine is elongate and forms an integral part of the upper caudal lobe. *Sternoptyx* shows a high degree of specialization with considerable reduction or fusion of elements. *Polyipnus* shares with *Maurolicus* (and *Vinciguerria*) the lack of fusion in hypurals 5 and 6. In some respects *Polyipnus* resembles the gonostomatid genera examined in size and shape of the uroneurals although, in general, it appears similar to *Argyropelecus*.

Axial skeleton (Figs. 8–11). While there is a similarity in structure and appearance of the vertebral centra in all genera examined, there are differences in neural and haemal spine pattern and structure. Posteriorly, the haemal and neural spine arrangement is symmetrical in all cases. In *Maurolicus* and *Valenciennellus* both spines are relatively long, unflattened, and tapering. The sternoptychid genera show a definite broadened and flattened condition particularly evident at the distal end. *Polyipnus* and *Argyropelecus* are alike in this respect. *Sternoptyx*, with considerable elongation of the posterior neural and haemal spines, reflects an independent and highly modified condition. *Vinciguerria* (Ahlstrom and Counts, 1958) appears more similar to *Polyipnus* than either of the gonostomatids examined.

Anteriorly, the symmetrical pattern of haemal and neural spines continues in *Valenciennellus* with no marked transitional region. However, in *Maurolicus* and the Sternoptychidae, there is an area of transitional vertebrae which is peculiar. There is a reduced, although fully formed, plural rib-bearing member followed by a number of characteristic haemal spines which may or may not be arched. This series of spines carries at least one pair

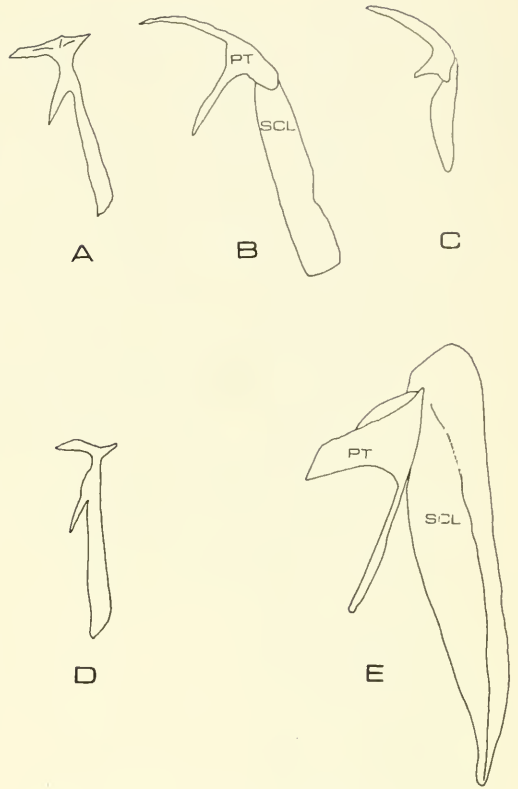


Figure 2. Post-temporal and supracleithrum: A. *Argyropelecus aculeatus*; B. *Maurolicus muelleri*; C. *Valenciennellus tripunctulatus*; D. *Polyipnus asteroides*; E. *Sternoptyx pseudobscura*. Abbreviations: PT = post-temporal; SCL = supracleithrum.

of greatly reduced or vestigial ribs. In *Maurolicus*, the first arched haemal spine is somewhat flattened distally. *Polyipnus* and *Argyropelecus* show a marked broadening of the distal end of these anterior haemal spines, with an increase in length proceeding posteriorly. *Sternoptyx* has a shortened flat first haemal spine; however, the posterior spines are elongate and not characteristically flattened.

The neural spines posteriorly are long, thin, and tapering in *Maurolicus* and *Valenciennellus*. As before, the sternoptychids show a broadened pattern unlike the above gonostomatids. *Polyipnus* and *Argyropelecus* are remarkably similar in this region.

The articulation of ribs is similar in all species, as well as the presence of reduced or vestigial pleural ribs, probably an indication that many more centra were rib-bearing in more primitive forms (see Weitzman, 1967b: 518). *Maurolicus* has a higher number of pleural and reduced pleural ribs than the sternoptychids. The latter are quite distinctly separated from *Maurolicus* and *Valenciennellus* by the presence of six or seven greatly broadened and lengthened pleural ribs which form a heavy protective cage around the now expanded visceral cavity. The number of abdominal vertebrae (the first caudal vertebra is defined as the anteriormost vertebra with a complete haemal arch) is relatively constant in the *Sternoptychidae* at about eleven (one specimen of *Polyipnus asteroides* had ten; Kotthaus (1967) reports twelve for *P. meteori*). Sample sizes were small, however.

Dorsal blade (Figs. 8–11). Weitzman (1967b) reported that the anteriormost pterygiophore of the dorsal fin consists of at least two fused pterygiophores in *Vinciguerria*. This same characteristic is found in *Maurolicus* which, in addition, has a number of pterygiophores that do not bear fin rays anterior to the fused one. The sternoptychids have this same basic feature, but have further modified it into essentially a "spinous dorsal." In *Polyipnus*, the fused pterygiophore is extended above the dorsal body surface and is spinose at the distal end. The anteriormost pterygiophores are enlarged, and closer together and more extensively allied to the supporting neural spines than they are in *Maurolicus*. These anterior pterygiophores become even more enlarged and closely allied, extend further above the dorsal surface, and with the fused pterygiophore form an extensive, sharp, dorsal blade in *Argyropelecus*. *Sternoptyx* retains the *Maurolicus* configuration anteriorly, but the fused pterygiophore becomes considerably extended and modified into a large dorsal spine.

Pelvic girdle (Figs. 8–11). In *Maurolicus* (also *Vinciguerria*, Weitzman, 1967b), the basipterygia are located even with or below the ventral margin of the pleural ribs. The paired basipterygia lie almost horizontally above the ventral body surface and are not closely joined to any rib element. With the broadening and deepening of the anterior thoracic region in the sternoptychids, the pelvic girdle has become a major structural element for the midregion of the trunk. *Polyipnus* exhibits a more intermediate condition than *Sternoptyx* and *Argyropelecus*. In the former, the basipterygia are oriented at approximately 45° to the ventral body surface and are located between the posteriormost large pleural ribs. There is now a relatively long ventral extension which ends in a spine protruding below the ventral body surface. The pattern becomes more pronounced in *Argyropelecus*. In this instance, the basipterygia are closely allied to each other and to the posteriormost large pleural rib. In some cases, the basipterygia are fused (*A. hemigymnus*) and the last pleural rib may become further enlarged for support (*A. aculeatus*). The ventral spiny process has also become more pronounced. *Sternoptyx* exhibits essentially the same evolutionary trend as *Argyropelecus*, with the fused basipterygia extending dorsally for a considerable length along the pleural ribs.

Pectoral girdle (Figs. 8–11). The pectoral elements, their general location and shape, are similar in all genera examined and include a well-developed mesocoracoid (see Weitzman, 1967b: 519). *Polyipnus* and *Argyropelecus* have an extended posterior flange of the cleithrum which protects and strengthens the pectoral area. The ventral margin of this flange has a characteristic spinose edge. The flange is noticeably reduced in *Sternoptyx*.

A forked post-temporal and well-developed supracleithrum are present in all genera (Fig. 2). *Polyipnus* and *Argyropelecus* are unique in that these two bones

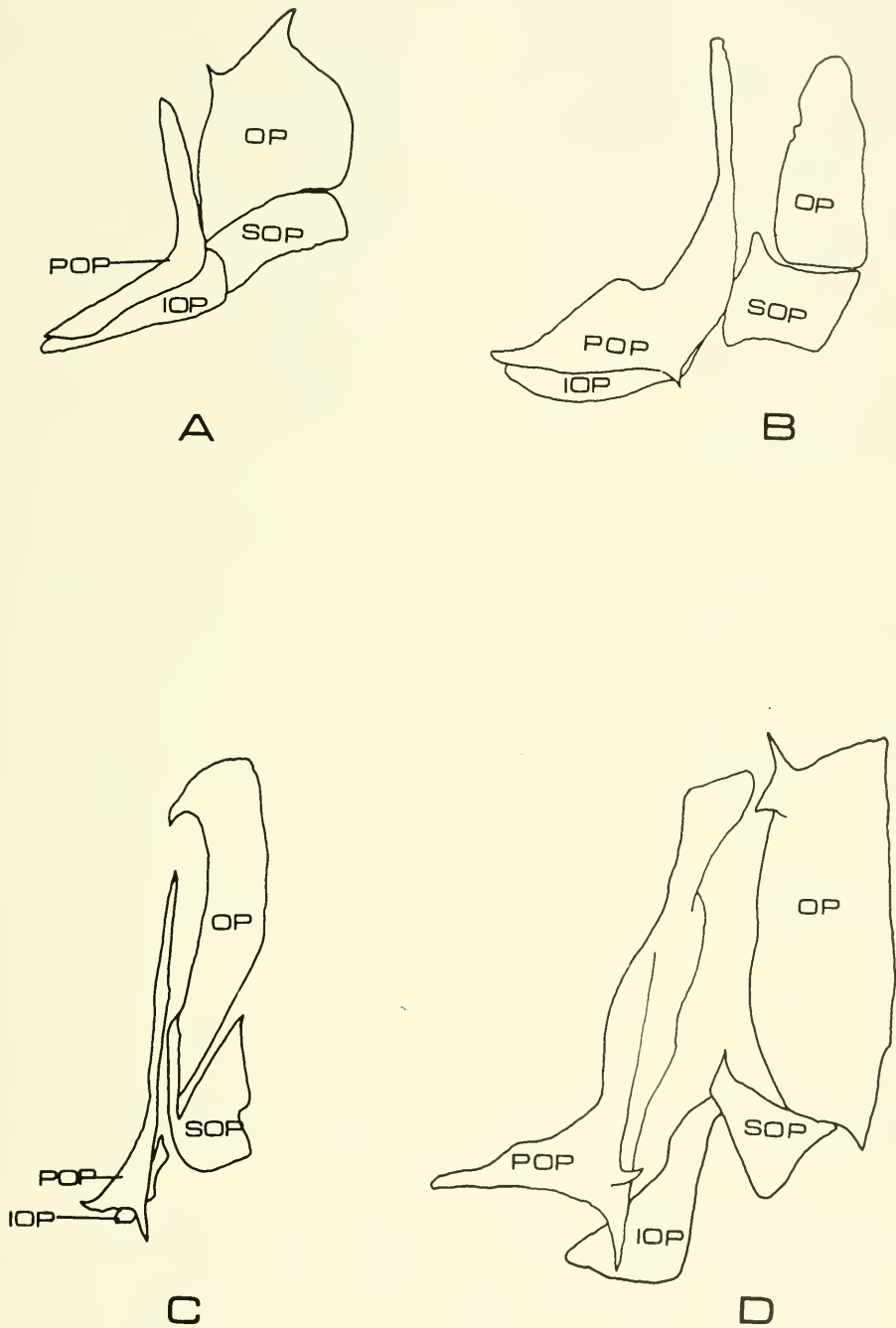
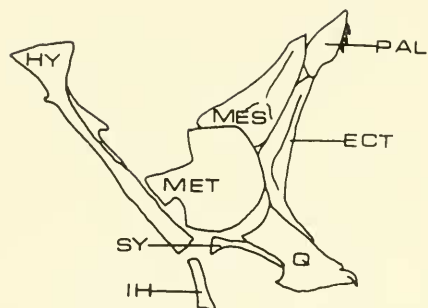
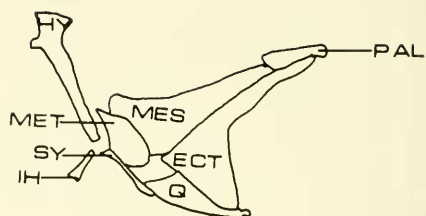


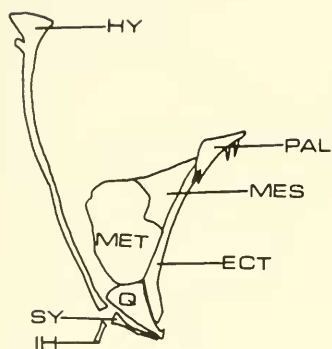
Figure 3. Opercular Series: A. *Maurolicus muelleri*; B. *Polyipnus asteroides*; C. *Sternaptyx pseudobscura*; D. *Argyropelecus hemigymnus*. Abbreviations: IOP = interopercle; OP = opercle; POP = preopercle; SOP = subopercle.



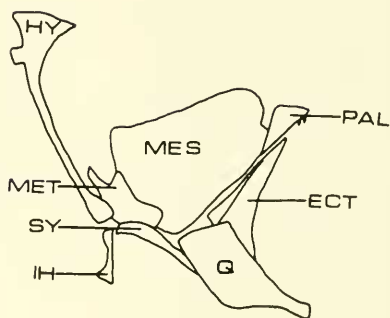
A



B



C



D

Figure 4. Suspensorium: A. *Polyipnus asteroides*; B. *Maurolicus muelleri*; C. *Sternoptyx pseudobscura*; D. *Argyropelecus hemigymnus*. Abbreviations: ECT = ectopterygoid; HY = hyomondibular; IH = interhyal; MES = mesopterygoid; MET = metapterygoid; PAL = palatine; Q = quadrate; SY = symplectic.

are fused. The post-temporal half of this process extends posteriorly above the dorsal body margin and bears spines. In certain species of *Polyipnus* these spines may become quite elaborate. In *Sternoptyx*, which has no such fusion, the post-temporal is forked and enlarged, and the

whole structure reflects a different evolutionary development.

Opercular series (Fig. 3). There is a classic opercular series present in the genera examined, with an interopercle below the ventral margin of the preopercle. There appears to be an evolutionary trend

from *Maurolicus* through *Polyipnus* to *Argyropelecus*. In *Polyipnus*, the interopercle is similar in shape to *Maurolicus*, but somewhat less broad. The preopercle has developed a ventral spine. A reduction in the anterior process of the interopercle, which now covers only the posterior ventral margin of the preopercle, may be observed in *Argyropelecus*. The preopercle, while similar in form to *Polyipnus*, has a lateral spine in addition to the ventral. *Sternoptyx* is somewhat independently modified with elongation and reshaping of the opercle and preopercle. The interopercle is similar to *Argyropelecus*, and the preopercle has a single ventral spine.

Upper jaw. The upper jaw, considering its close relation to feeding ecology, is somewhat similar in *Maurolicus*, *Polyipnus*, and *Argyropelecus*. There are two characteristically shaped supramaxillae, a well-developed toothed maxilla and premaxilla. The premaxillae have short ascending processes (as does *Vinciguerrria*). The maxilla, included in the gape to a small degree, is markedly broadened posteriorly in *Polyipnus*, and the whole jaw apparatus reflects a peculiar method of feeding. *Sternoptyx* is quite different. In this instance the maxilla is heavily toothed and the major upper jaw bone in the gape. The premaxilla is small, although toothed, and has no ascending process. The second supramaxilla has been lost.

Suspensorium (Fig. 4). There appears to be a general evolutionary trend in the Sternoptychidae in which the suspensorium migrates from behind and slightly below the posterior orbital region, ventrally and anteriorly to a point directly below the anterior half of the orbit. This trend can be seen by examining the ratio of quadrate length to hyomandibular length: *Maurolicus*, 1:1.25; *Polyipnus*, 1:1.5; *Argyropelecus*, 1:2.5; *Sternoptyx*, 1:7.4. The metapterygoid bone is proportionately smaller in *Maurolicus* and *Polyipnus*, and the mesopterygoid is greatly enlarged in

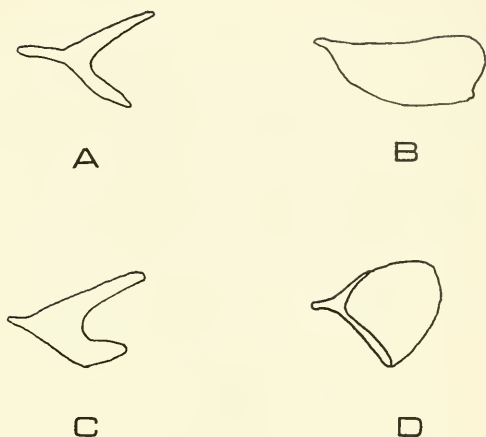


Figure 5. Urohyal: A. *Sternoptyx pseudobscura*; B. *Maurolicus muelleri*; C. *Argyropelecus sladeni*; D. *Polyipnus asteroides*.

the latter. This again reflects the peculiar jaw morphology in this genus.

Hyoid (Fig. 5). The most notable hyoid feature is the gradual reduction of the platelike posterior extension of the urohyal in the sternoptychids. *Polyipnus* illustrates an intermediate condition, while *Sternoptyx* and *Argyropelecus* show complete reduction to a Y-shaped bone.

Chondrocranium. The curvature of the parasphenoid exhibits a continuous gradation from a nearly horizontal position in *Maurolicus* to the extreme right-angled bone in *Sternoptyx*. The presence and degree of ossification of the basisphenoid is variable. It is well developed and has two centers of ossification in *Valenciennellus*. Only the dorsal ossification remains in *Maurolicus*, while the bone is absent in *Argyropelecus*. *Polyipnus* and *Sternoptyx* have well-developed basisphenoid bones.

The neurocranium (Fig. 6) is generally conservative when viewed as a whole. The shape, relative size, and location of the bones are similar in all genera examined. The neurocranium resembles *Vinciguerrria* (Weitzman, 1967b), especially in the general shape and location of the sphenotics, pterotics, and epiotics. Important features

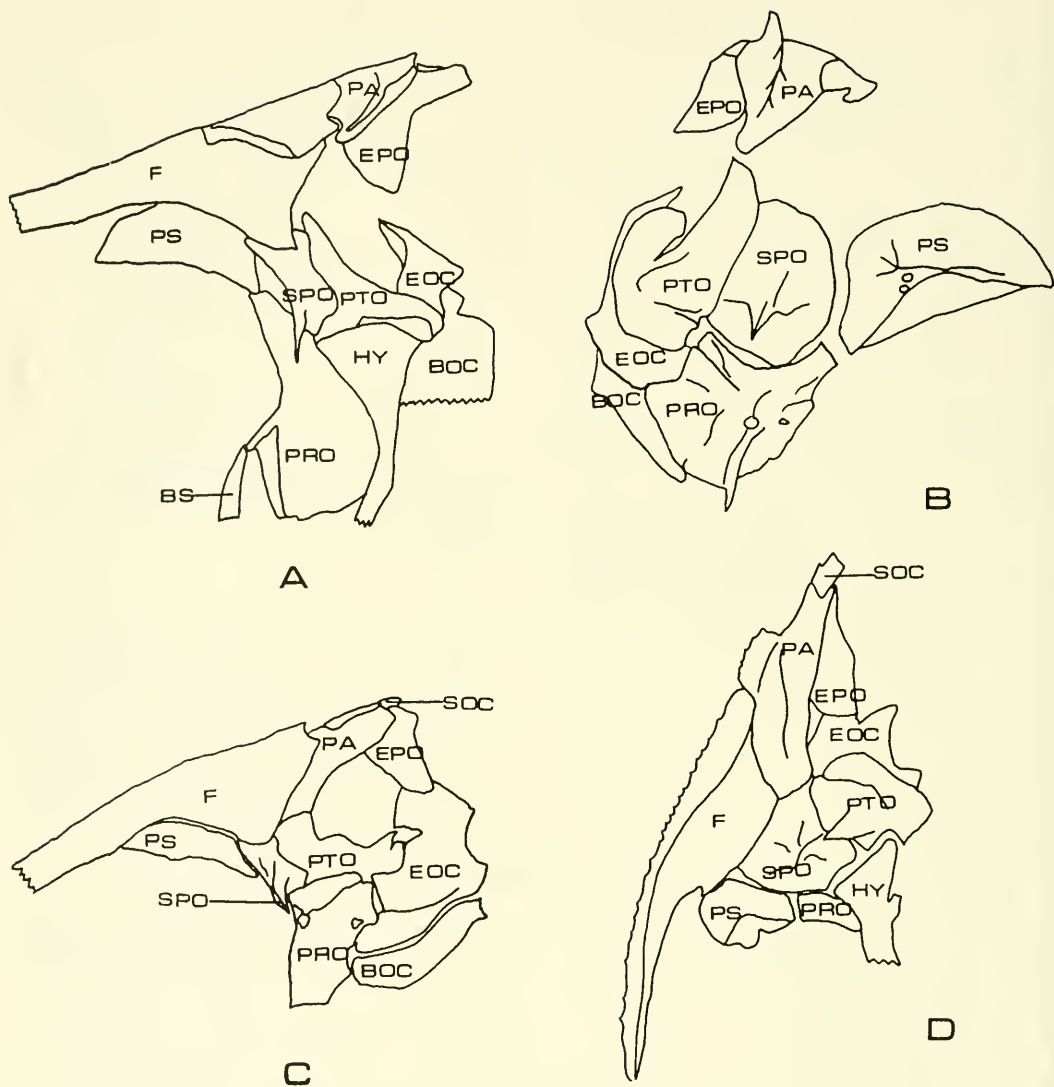


Figure 6. Neurocranium (lateral view): A. *Polyipnus asteroides*; B. *Argyropelecus hemigymnus* (frontals removed); C. *Maurolicus pennanti*; D. *Sternoptyx pseudabscura*. Abbreviations: BOC = basioccipital; BS = basisphenoid; EOC = exoccipital; EPO = epiotic; F = frontal; HY = hyomandibular; PA = parietal; PRO = prootic; PS = pterosphenoid; PTO = pterotic; SOC = supraoccipital; SPO = sphenotic.

are: the epiotics meet below the supraoccipital in sternoptychids, while there is no tendency in this direction in *Maurolicus* and *Valenciennellus* (Fig. 7); the presence of well-developed parietals with dorso-lateral ridges in sternoptychids, but not in other genera examined; the presence of

a well-developed alisphenoid (pterosphenoid) bone in all genera; and the progressive tendency for the neurocranial axis, as measured along the frontal, to assume a more vertical configuration from *Polyipnus* to *Sternoptyx*. There is considerable development of the otic region in *Polyipnus*

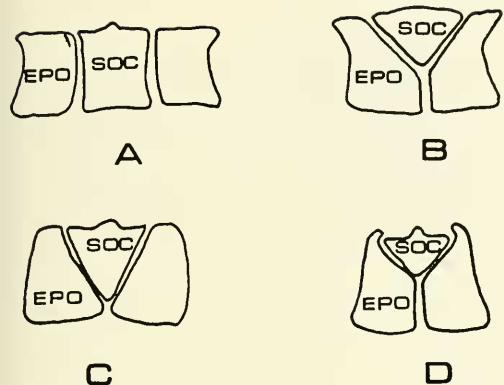


Figure 7. Epiotic-Supraoccipital Relationship (posterior view): A. *Maurolicus muelleri*; B. *Polyipnus asteroides*; C. *Sternoptyx pseudobscura*; D. *Argyropelecus hemigymnus*. Abbreviations: EPO = epiotic; SOC = supraoccipital.

which contains peculiarly shaped and very large otoliths (Kotthaus, 1967).

Abdominal keel scales (Figs. 8–11). *Polyipnus* and *Argyropelecus* have developed ossified plates (modified scales) which form a keel and serve to give structure to the abdominal region and associated photophore groups. Several plates appear posterior to the pelvic fins; most are anterior to them. The plate size, number, and distance between plates is less well developed in *Polyipnus*. *Sternoptyx* seems also to have a keel-like structure, but this is not ossified. The gonostomatids examined have little keel development and no ossification in this region.

Anal pterygiophores (Figs. 8–11). In sternoptychids, the anal pterygiophores show a characteristic gap. Several pterygiophores are associated with and between the same haemal spine forming a circular gap. In this respect the *P. spinosus* species complex is the least well developed. In the gonostomatids examined there is one pterygiophore for each haemal spine with no gap. The anteriormost anal pterygiophore possesses flangelike processes projecting laterally in *Polyipnus*, *Sternoptyx*, and *Maurolicus*. The former two have, in addition, pronounced ventral processes lacking in *Maurolicus*. *Argyropelecus* has

no processes, although the anal pterygiophores are enlarged.

Photophores. The glandular nature and pattern of photophores seem to indicate some relationship among all genera studied. The trend appears to be from a condition of an essentially unbroken row of photophores on the ventral body surface (*Maurolicus*) to one in which this row is broken both horizontally and vertically (sternoptychids). As before, *Polyipnus* is intermediate in this respect.

OSTEOLOGICAL CONCLUSIONS

The osteological results lead to the following conclusions. The present definitions of the family (e. g., Regan, 1923; Schultz, 1961; and Morrow, 1964) and included genera are inadequate, often seriously in error, and require revision. The Sternoptychidae appear to be derived from some antecedent of the primitive genus *Maurolicus*. The genera *Sternoptyx*, *Argyropelecus*, and *Polyipnus* form a separate taxon. Each of these genera has probably been distinct for a long period, as each shows a great deal of divergence and independent evolution.

From the evidence above there is little doubt that the two maurolicid genera and the Sternoptychidae are closely related. The traditional differences such as absence of a mesocoracoid and alisphenoid (pterosphenoid), curved parasphenoid, and even the particulars of the dorsal blade have been found to be, wholly or in part, similarities rather than differences. Basic differences do exist, however, and in general follow from Hermann's original characterization of the Sternoptychidae as fish having a deep, highly compressed body form. It is this striking evolutionary pattern that gives rise to many of the following character complexes which separate the present Sternoptychidae from those gonostomatids examined.

1. Modification of the first neural spine, appearing as a short, triangulate, vertical blade with further modification of the



Figure 8. *Maurolicus muelleri*: R/V CHAIN, Cruise 17, RHB 804; 10° 52' N; 29° 26' W.

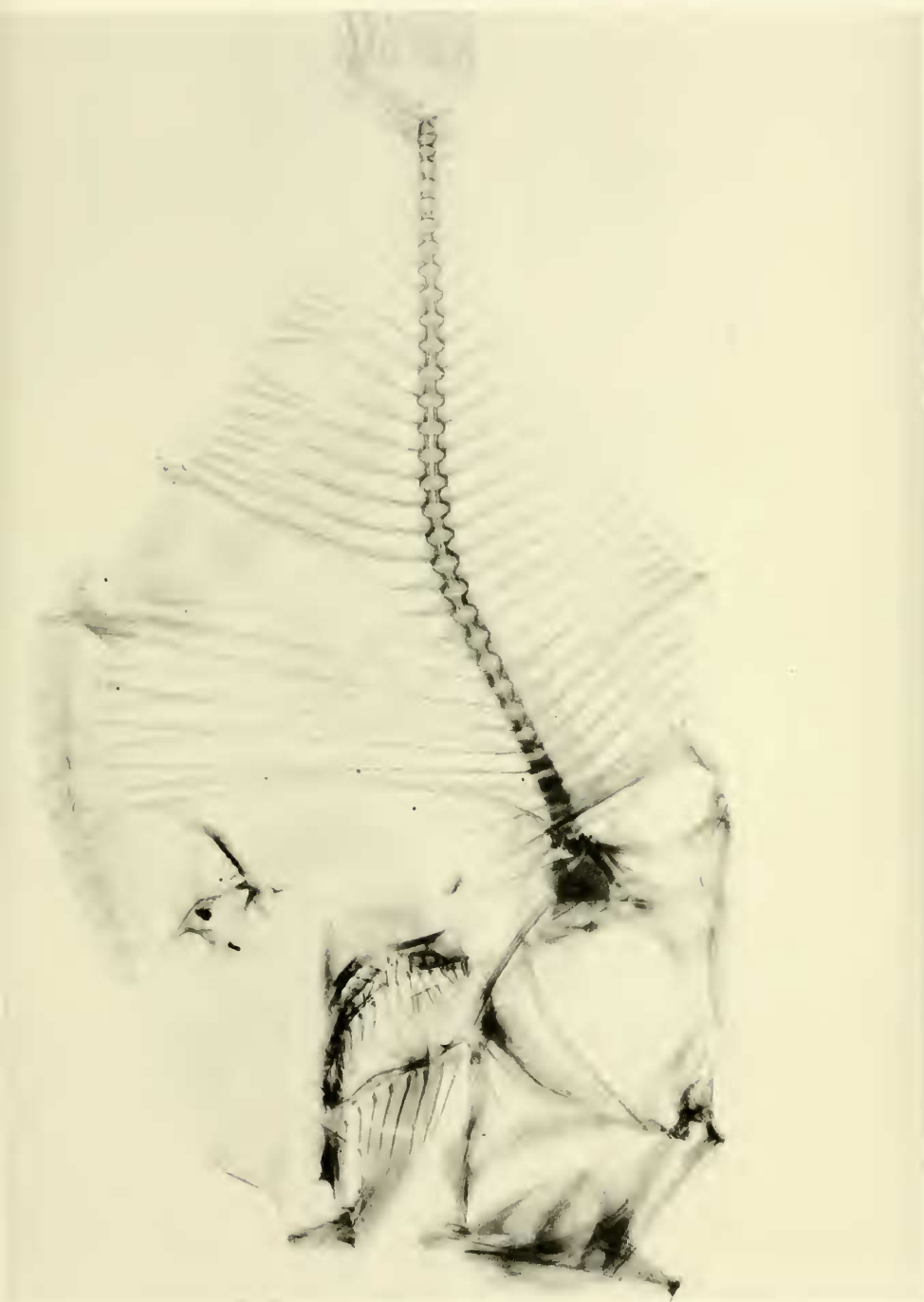


Figure 9. *Polyipnus osteroides*: R/V CHAIN, Cruise 60, RHB 1295; 22° 22' N; 95° 20' W.



Figure 10. *Siemaplyx pseudobscura*: R/V CHAIN, Cruise 35, RHB 977; 01° 20' S; 27° 37' W.



Figure 11. *Argyropelecus olfersi*: USNS ELTANNIN, Station 1769; 36° 05' S; 133° 00' W

second neural spine to serve as a supporting element. (In the *P. spinosus* species complex, the second neural spine resembles the first.)

2. Characteristic broadening and flattening of the haemal and neural spines in the posterior caudal region.

3. The presence of six or seven large, heavy, pleural ribs with relatively few reduced or vestigial ribs. This includes a low number (10–12) of abdominal vertebrae.

4. Development of the dorsal pterygiophore system into a "blade" or spine.

5. A vertically oriented pelvic girdle, the basipterygia bearing spines, sometimes fused, and closely allied to the heavy pleural ribs.

6. A preopercle with a well-developed ventral spine.

7. A heavy, forked, post-temporal which is fused to the supracleithrum in *Argyropelecus* and *Polyipnus*, forming a spiny extension dorsally.

8. A progressive migration forward of the suspensorium.

9. Reduction of the bony extension of the urohyal.

10. Epiotics meeting below the supraoccipital and the presence of well-developed, ridged parietals.

11. Presence of a well-developed abdominal keel-like structure which is ossified in *Argyropelecus* and *Polyipnus*.

12. Presence of a circular gap in the anal pterygiophore series, these pterygiophores being enlarged.

13. Presence of ventral processes on the anteriormost anal pterygiophore in *Sternoptyx* and *Polyipnus*.

14. Marked similarity of photophore pattern and number.

Some of these character complexes are not radically different from the gonostomatids examined, and there is a degree of convergence and parallel evolution which is difficult to appraise. Taken as a whole, however, they strongly suggest that the sternoptychid genera have reached a com-

mon evolutionary grade, typified by their peculiar body form, and by which they differ from the more generalized and primitive maurolicid gonostomatids.

While acknowledging that the Sternoptychidae are a specialized offshoot of maurolicid or premaurolicid stock, for the following reasons I do not feel justified in combining the Gonostomatidae and Sternoptychidae as some have suggested.

The present family Gonostomatidae is an unwieldy one which involves many diverse types and requires extensive revision (Weitzman, personal conversation). The problem of gaps, their size and importance, cannot be adequately answered without further study within the Gonostomatidae. Osteologically, the Sternoptychidae have reached an evolutionary grade peculiar to themselves and one quite distinct in several major ways from the gonostomatids examined. Using for a guideline the family concept as it is generally employed by Mayr, Linsley, and Usinger (1953), it appears that the Sternoptychidae do have an ecological, or at least adaptive, distinctness.

The adaptive distinctness concerns the peculiar body shape and its possible functional significance. There are at least two major adaptive features involved. The first deals with the ideas and evidence presented by Denton and Nicol (1965) and Nicol (1967) on the relationship between silvery color and body shape in teleost fishes. The midwater environment is one in which the distribution of daylight is independent of the altitude of the sun and cloudiness of the sky, and light distribution is essentially symmetrical about a vertical to the surface. Furthermore, the Sternoptychidae have brilliant, silvery sides. All fish species with these features so far examined (Denton and Nicol, 1965; Nicol, 1967) have layers of reflecting platelets which are oriented to make the fish as invisible as possible. It may be assumed that the same is true with hatchetfish. There is a change in reflectivity with body rotation in the several Sternoptychid

species examined. A silvery fish which is flattened laterally, having very little inclined ventral surface will approach the ideal in camouflaging (see Denton and Nicol, 1965: 717). The Sternoptychidae could thus serve as a living model for such a body form.

The second adaptive feature concerning body shape is the development of heavy structural ossifications and spines, especially the dorsal "blade." Spines have developed in fish, presumably, for protection. The sternoptychids have several extensive spine complexes: post-abdominal, post-temporal, preopercle, and dorsal. The spines are rigidly braced and the whole body strongly ossified, resulting in a compact rigid body shape. A spinous dorsal has developed somewhat analogous to that of the higher Perciform fishes. This, coupled with the expanded abdominal region, results in a high length-to-depth ratio (Table 1).

In an environment populated by a host of predators, many with special adaptations for ingesting large prey items, an increase in the length-to-depth ratio of a prey should be advantageous. A predator normally capable of swallowing *Valenciennellus* would require an approximate threefold increase in mouth diameter in order to accommodate *A. hemigymnus* of the same length (Table 1). Ossification also takes place quite early. Juveniles or prejuveniles of about 10 mm have well-developed spines and are ossified.

Phylogenetic relationships. The question of a monophyletic origin of the hatchetfish is unanswerable. The three genera show a great deal of divergence and independent evolution even within genera. Using the character complexes examined, some comments about generic relationships can be made, however.

The family appears primitive and probably originated from a premaurolicid ancestor, possibly something between the very early *Vinciguerria* and *Maurolicus*. Most of the characters examined could

have been derived from a form somewhat intermediate to the above genera.

The genus *Sternoptyx* seems to have diverged quite early from the line or lines leading to *Polyipnus* and *Argyropelecus*. It then continued to evolve independently, resulting in the present highly specialized form. In almost every case, *Sternoptyx* shows marked differences. The presence of a basisphenoid, the characteristically shaped, enlarged, first anal pterygiophore; the simple anterior, dorsal pterygiophores; possibly the meeting of the parietals, and the unfused post-temporal and supracleithrum all appear primitive. These characters are also shared with *Polyipnus* with the exception of the unfused post-temporals and meeting parietals. The presence of a small premaxilla and large maxilla as the major jaw bone in the gape are generally regarded as primitive. However, jaws and dentition have varied considerably in gonostomatids (Grey, 1964), and this may be a secondary phenomenon. The disappearance of the anterior pedicels of the premaxilla and loss of the second supramaxilla can be explained in the same way, especially since the orbital region seems to have undergone considerable expansion. The resemblance of the urohyal to *Argyropelecus* may again be the result of parallel or convergent evolution involving feeding ecology which is similar in these genera.

Evolution from a premaurolicid ancestor can be traced somewhat more directly in the case of *Polyipnus* and *Argyropelecus*. *Polyipnus* and *Argyropelecus* share several character complexes: the characteristic blade-shaped, caudal haemal spines; the presence of the double pterygiophore as the major element in the "blade"; the presence of ossified, bony keel plates; the fusion of the post-temporal and supracleithrum; and separation of parietals by the supraoccipital (known to be variable in the Gonostomatidae). *Polyipnus* appears intermediate between *Maurolicus* and *Argyropelecus* in several characters:

TABLE 1. BODY DEPTH AND STANDARD LENGTH MEASUREMENTS.

Family	Species	SL (mm)	Maximum Body Depth* (mm)
Gonostomatidae	<i>Danaphos aculatus</i>	38.0	9.2
	<i>Valenciennellus tripunctatus</i>	26.0	5.4
Sternoptychidae	<i>Argyropelecus hemigymus</i>	38.0	24.0
	<i>Argyropelecus hemigymus</i>	26.0	16.9

* Includes dorsal blade.

the axial skeleton in general; anterior dorsal pterygiophore development; pelvic girdle modification; evolution of the cleithrum, first branchiostegal rays, and urohyal; the opercular series, especially the preopercle and interopercle; suspensorium development; parasphenoid curvature, and progressive deepening and shortening of the body with reduction in a long unbroken series of ventral photophores. *Polyipnus* has characters that are not shared with *Argyropelecus* in addition to those which are shared with *Sternoptyx*. These include: hypurals 5 and 6 unfused (3 and 4 also in the *P. spinosus* complex); small, relatively unmodified dentition; and, a urostylar element with several unfused post-terminal centra.

Polyipnus also has several highly specialized characters: the peculiar jaw morphology; a greatly enlarged otic region with characteristically shaped, large otoliths (Kotthaus, 1967); and, the peculiar development of the cleithrum (pectoral shield).

The divergence of *Polyipnus* and *Argyropelecus* has involved the continued evolution of many intermediate characters mentioned above. Other major developments in *Argyropelecus* are: fusion of hypurals 5 and 6 and the post-terminal centra; the presence of seven rather than six heavy pleural ribs; development of a lateral preopercular spine (one species of *Polyipnus* has this); development of a fanglike dentition; loss of the basisphenoid; loss of the flangelike process on the first anal pterygiophore; and, the development of telescopic eyes.

Because the number of character complexes examined was limited, the suggested phylogeny is only a tentative one. The family consists of three divergent, independently specialized genera. *Polyipnus* appears the most primitive, *Sternoptyx* the most highly specialized and the most difficult to place, while *Argyropelecus* falls somewhere in between.

THE FOSSIL RECORD

The earliest reported sternoptychid fossil is from the Eocene of the Dabakhan beds of Georgia, USSR (Daniltschenko, 1962). The fossil, *Polyipnoides levis*, is not well preserved and many important characters cannot be appraised. It does have long pleural ribs and a characteristic broadening of the body anteriorly. The post-temporal, however, is unlike any modern sternoptychid. The dorsal "blade" or pterygiophore development is absent and the jaws seem more gonostomatidlike, although this is difficult to determine with certainty. The neural and haemal spines show little characteristic flattening, and the frontals do not exhibit the heavy development characteristic of the hatchetfish. Consequently, it appears that while this fossil could be a proto-sternoptychid fish, I cannot accurately place it with the present Sternoptychidae or Gonostomatidae.

Polyipnus sobniowiensis was reported from the Jaslo shales of Poland (Jerzmańska, 1960; Jerzmańska and Jucha, 1963) and dates as late Eocene-early Oligocene. Enlarged pleural ribs with a general broadening of the body anteriorly are present in this species. Pterygiophore development

anterior to the dorsal fin rays is definite, and there is evidence of very slight, dorsal blade development. Some photophore groups conform roughly to modern *Polyipnus*, although the fossil supra-abdominal group is more numerous. The cleithrum displays the marked ventral curve typical of the Sternoptychidae and the maurolicid-gonostomatids. There is, however, little flattening of haemal and neural spines. The pelvic girdle, while partially vertical, is still below the rib line, and the body shape, while somewhat broad, is more similar to the maurolicid gonostomatids. There is no spine on the preopercle, the orbit shows no great expansion, and there are no signs of keel plates. This fish, while it has some sternoptychid characters, appears essentially to be maurolicid-gonostomatid. Consequently, its place in the genus *Polyipnus* is questionable, although it may be near the basal stock which gave rise to modern hatchetfishes.

Pauca (1931) described *Sternoptyx prisca* from the lower Oligocene deposits of Piatra Neamț. The presence of a well-developed dorsal "blade," heavy cleithrum, and pleural rib characteristics place it in the genus *Argyropelecus*. If the dating is correct, it represents the earliest known fossil of this genus.

By Oligocene, and certainly by Miocene times, several examples of the genus *Argyropelecus* were evident in Tethys deposits of Europe (Arambourg, 1929; Daniltshenko, 1960), and in various deposits of California (David, 1943). All of these fossils clearly represent members of the above genus, and *A. logearti* (Arambourg, 1929) appears to be closely related to the modern *A. hemigymnus*.

In the present study, three remarkable fossils from Miocene deposits in California were examined and compared with modern relatives.

Fossil A (Figure 12)

Description. SL 50 mm, body depth 26 mm; dorsal blade from its extension

above the dorsal fin origin, low; last pleural rib only slightly reinforced; anterior haemal spines not greatly flattened, postabdominal spines short, symmetrical, not markedly curved; transitional vertebrae two in number; anal pterygiophores relatively simple, not markedly broadened at distal end; anal pterygiophore gap contains two haemal spines; number of anal pterygiophores before gap, seven, after gap, four to five; hypurals 1 and 2 separate; number of vertebrae from posterior margin of dorsal blade to last neural spine, 29.

Fossil B (Figure 13)

Description. Similar to Fossil A above; number of vertebrae from dorsal blade to last neural spine, 30; hypurals 1 and 2 separate; postabdominal spines simple, symmetrical; posteriormost pleural ribs not greatly enlarged.

Fossil C (Figure 14)

Description. SL 60 mm, body depth 40 mm; number of vertebrae from posterior dorsal blade to last neural spine 26, possibly 27; both abdominal and trunk regions greatly broadened; hypurals 1 and 2 fused; anterior haemal spines broad, flat, blade-like; distal end of anal pterygiophores broad, gap well developed, circular, and includes two neural spines.

Fossils A and B are indistinguishable in both key characters and meristics from the modern species *A. affinis* (Fig. 15) and can be assigned to this species complex. Fossil A seems broader than the modern form, but the fossil appears distorted ventrally and there are no other obvious differences.

Fossil C is a member of the *A. lychnus* complex (Figs. 11 and 16). Osteologically there is little difference between *A. olfersi* and *A. lychnus*. However, the fossil has a relatively low dorsal blade, measured from the origin of the dorsal fin rays, a characteristic of *A. lychnus* (Fig. 16). The second transitional vertebra of Fossil C

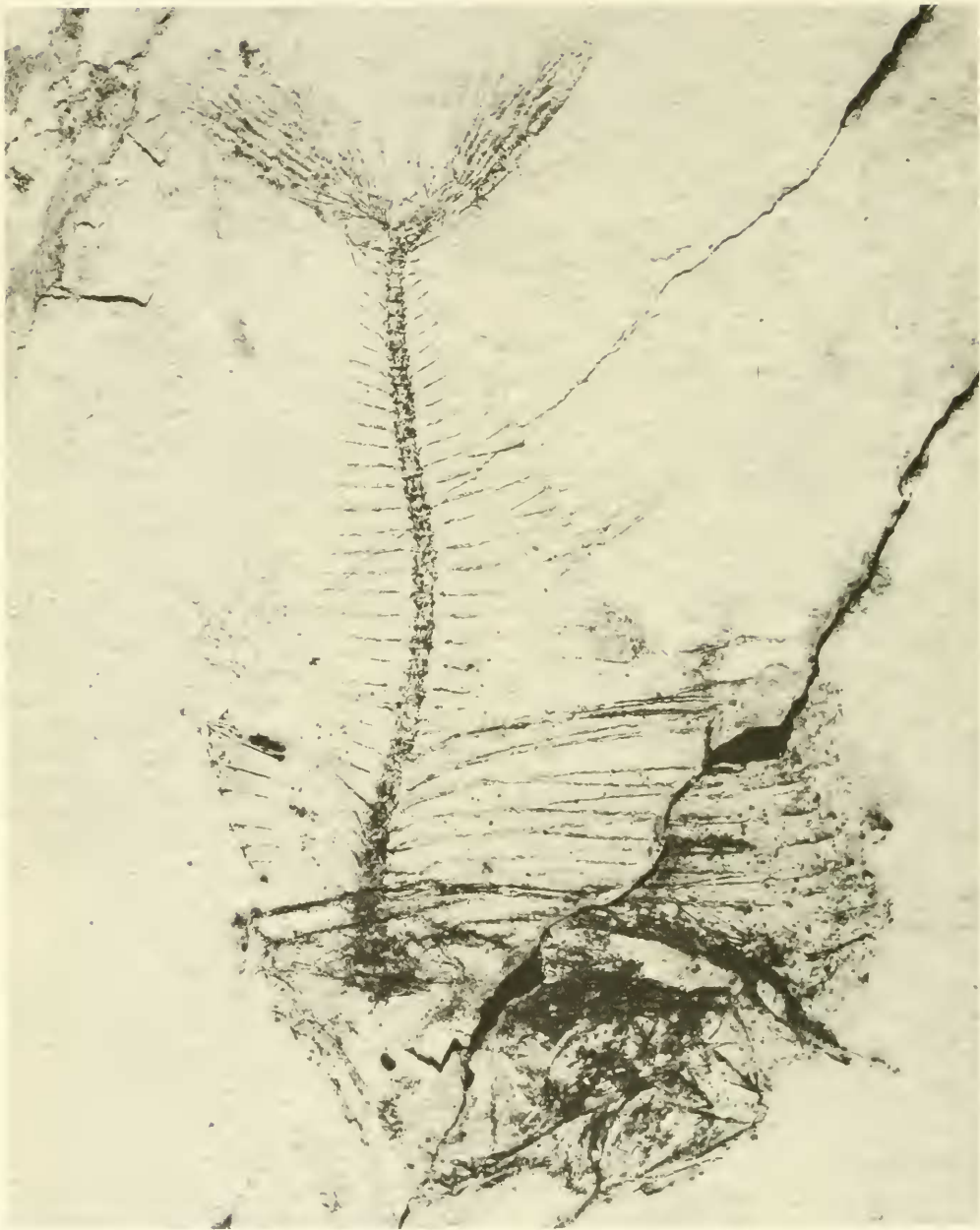


Figure 12. Fossil A. LACM 1925 (1A), Miocene, Cabrillo Beach, Palo Verde, California.

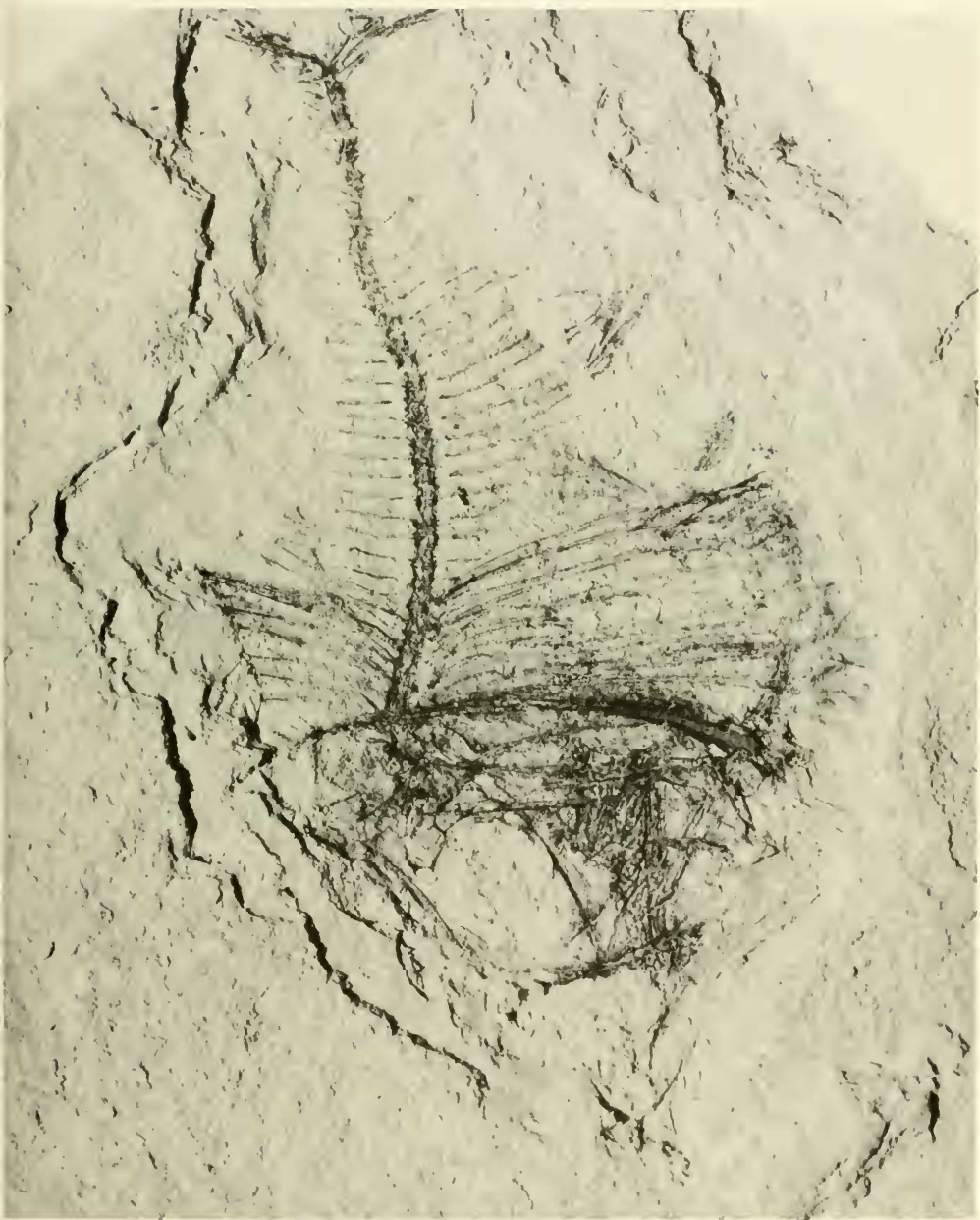


Figure 13. Fossil B. LACM 1925 (6), Miocene, Cibrillo Beach, Polo Verdes, California.

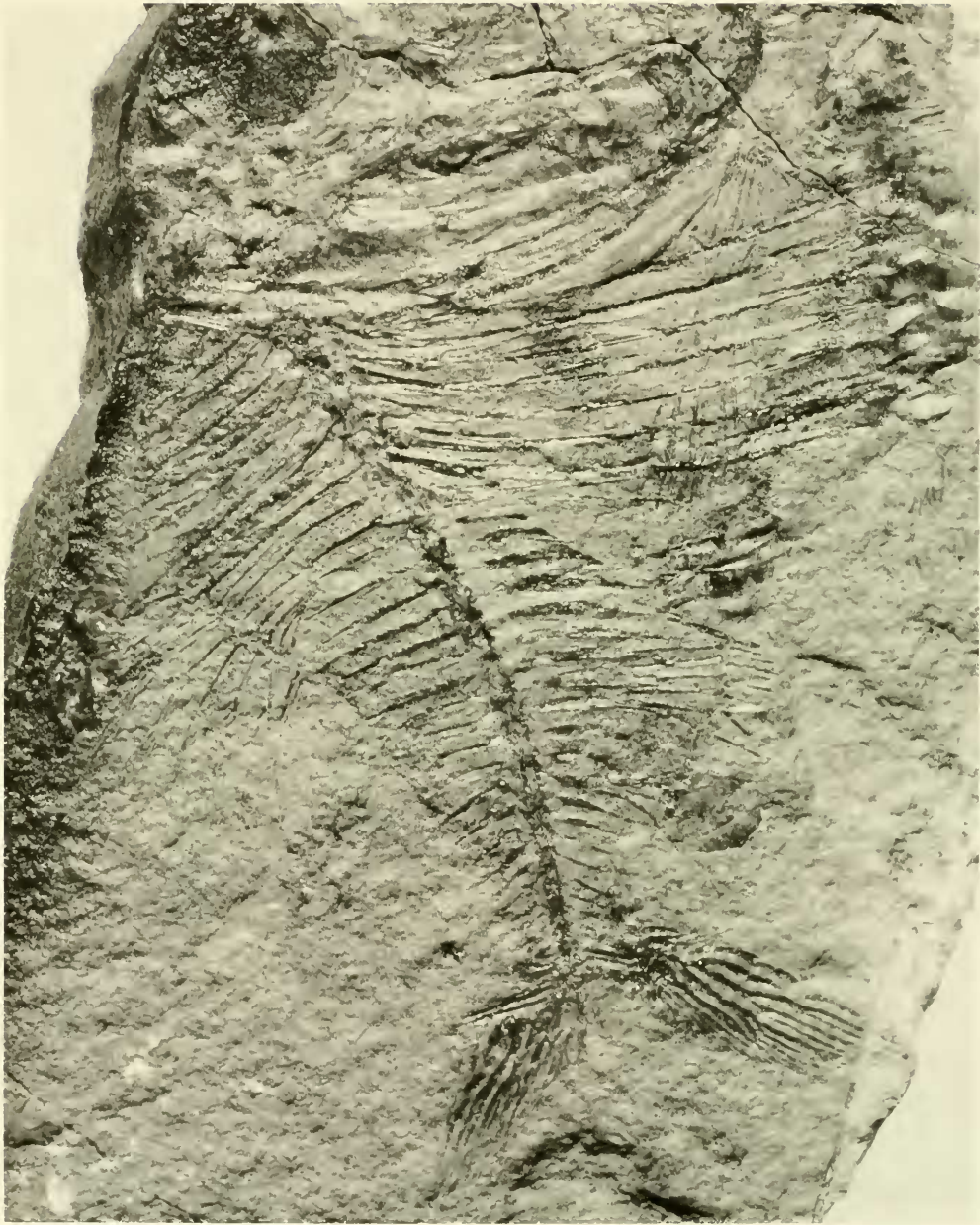


Figure 14. Fossil C. LACM (3), M. Miocene, Bluss Cove, near Malaga, Palo Verdes, California.

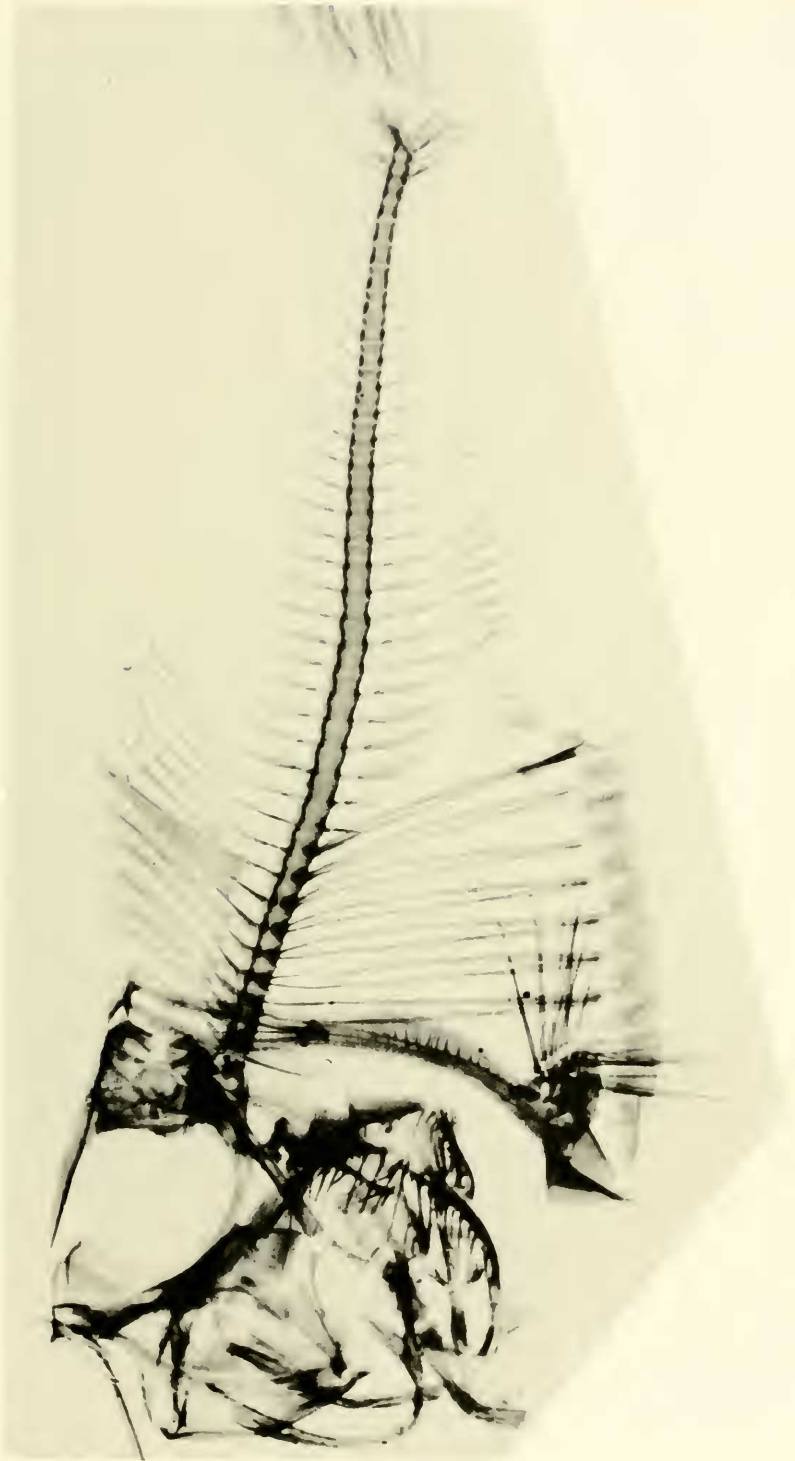


Figure 15. *Argyropelecus affinis*: R/V CHAIN, Cruise 60, RHB 1257; 13° 42' N; 70° 36' W.



Figure 16. *Argyropelecus lychnus*: R/V ANTON BRUUN, Cruise 13, Station 2; 33° 16' S; 72° 36' W.

KEY TO THE GENERA OF STERNOPTYCHIDAE

- 1a. Abdominal photophores 12; telescopic, dorsally oriented eyes; several dorsal pterygiophores form extensive blade anterior to dorsal rays genus *Argyropelecus* (p. 31).
- b. Abdominal photophores 10; eyes normal; dorsal blade consisting of only one or two spines from a single or two fused pterygiophores 2
- 2a. Anal photophores 3; no supra-abdominal photophores; single large dorsal spine with anterior serrate extension; first anal pterygiophore greatly enlarged, supporting tri-angulate transparent membrane above anal fin rays genus *Sternoptyx* (p. 67).
- b. Anal photophores 6 or greater; 3 supra-abdominal and a lateral photophore; dorsal blade reduced; no large transparent membrane above anal fin rays genus *Polyipnus* (p. 79).

has a pair of vestigial ribs whereas the one modern *A. lychnus* examined does not. One of the specimens of *A. olfersi* examined has small vestigial ribs on this vertebra; otherwise, all of the fossil characters and vertebral counts are identical to these modern species. Fossil C is probably *A. lychnus* or at least its immediate predecessor.

By mid-Miocene times evolution within the genus *Argyropelecus* was essentially complete and species distributions show modern characteristics. This genus with its many specializations must have originated by the late Eocene at the latest and possibly as far back as the Paleocene or late Cretaceous.

During or prior to the early Cretaceous, some members of the early salmonoid fishes began to adapt to a deep water environment. After the basic adaptations to this environment were acquired (at latest mid-to-late Cretaceous) there was considerable stomiatoid radiation which continued into the late Eocene to early Oligocene. This radiation led to many diverse forms, of which the maurolucid-gonostomatids were one. Within the latter, an ancestor, possibly resembling *P. sobnioviensis*, gave rise to a form or series of forms with many features of the modern genus *Polyipnus*. From this basic stock the modern genera evolved, conceivably quite rapidly. By the Miocene, evolution was practically complete in the specialized *Argyropelecus* and possibly the other genera as well. The stomiatoid-gonostomatid radiations of the early tertiary show evidence of being fairly complete by that

time also. Many modern gonostomatid genera were present during that time, and Miocene faunas have distinctly modern resemblances (David, 1943; Grey, 1964; Crane, 1966; Daniltschenko, 1960). The salmonoid-derived midwater fauna appears to have replaced earlier forms during the early Tertiary, and it remains the dominant element today.

SYSTEMATICS

Family STERNOPTYCHIDAE

Type Genus: *Sternoptyx* Hermann 1781

Diagnosis. Neural spine of first pre-terminal vertebra vertically oriented, broadened, with triangulate paddle shape, no fin rays attached; second preterminal vertebra modified for support of first (except *P. spinosus* complex); basipterygia vertically oriented, spine bearing, contained dorsally within, and closely joined to the ventral margin of the posterior pleural ribs; pelvic fin rays vertically oriented; six to seven pleural ribs enlarged to form an expanded rib cage; epiotics meet below supraoccipital; parietals well developed, bearing dorsolateral ridges; one or more dorsal pterygiophores enlarged to form blade or spinelike extension anterior to dorsal rays; anal pterygiophores form characteristic gap below anal photophore group; preopercle bearing well-developed ventral spine.

Description. Bright silvery colored, small fishes; standard length usually less than 90 mm; body deep, strongly compressed; bony scalelike plates form keel below ventral photophore groups (except

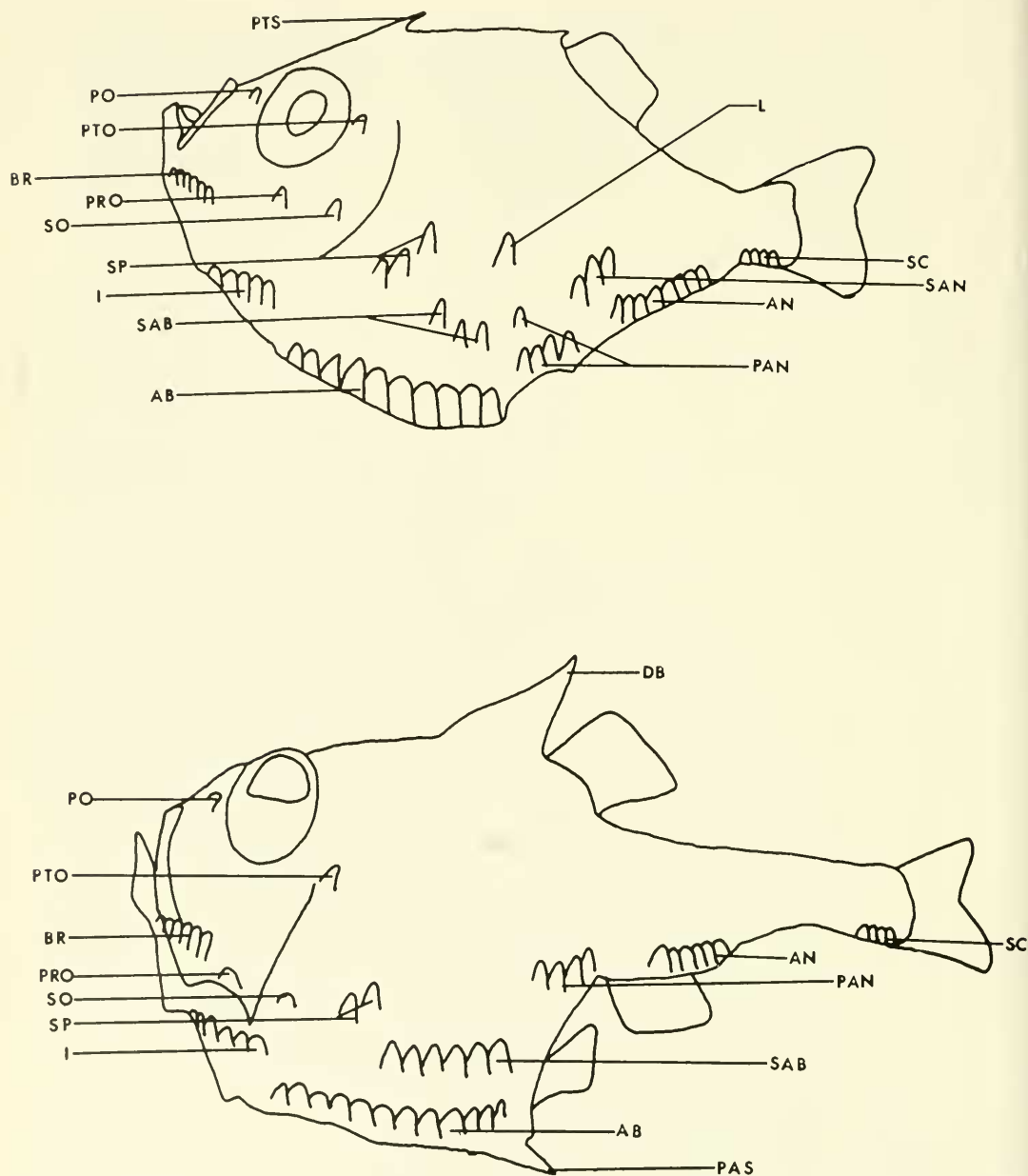


Figure 17. Photophore and spine characteristics: top—*Polyipnus*; bottom—*Argyropelecus*. Abbreviations—photophores: see p. 6; spines: DB = dorsal blade; PAS = postabdominal spine; PTS = post-temporal spine.

Sternoptyx); 10–12 abdominal, and four subcaudal photophores always present (see Figs. 17 and 18 for photophore and spine characteristics); nasal lamellae well developed; digestive tract simple, with thick

muscular stomach, five or more pyloric caecae, and short straight intestine; eyes large, well developed; gape vertical; adipose fin usually present; scales thin or absent except along ventral surface; swim

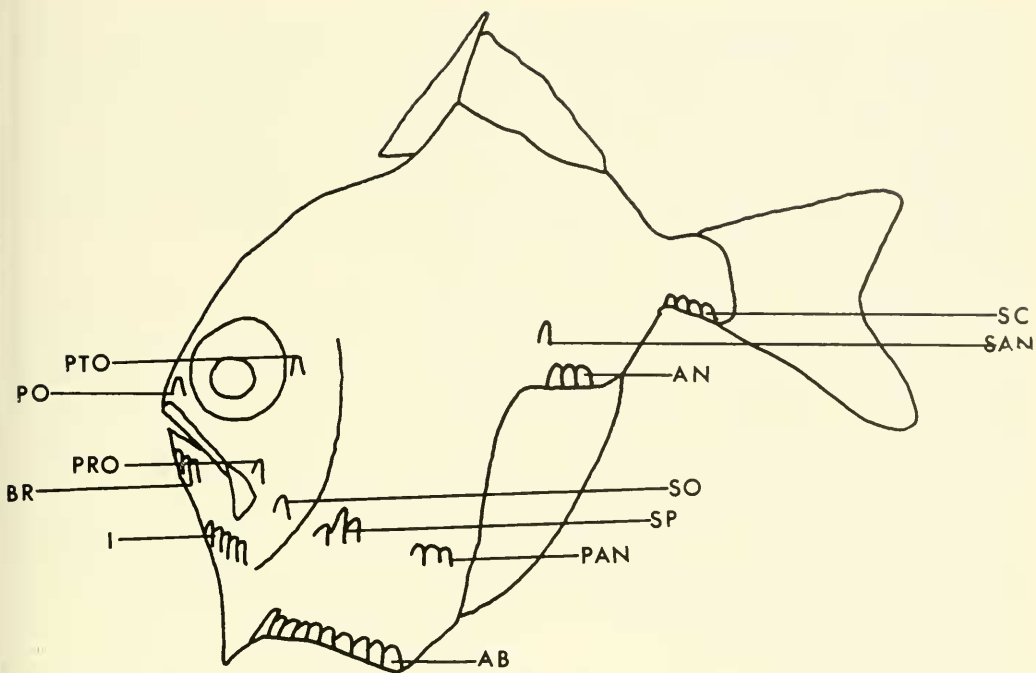


Figure 18. Photophore characteristics: genus *Sternoptyx*. Abbreviations: see p. 6.

bladder present (see above for osteological description).

Genus *Argyrolepecus* Cocco, 1829

Argyrolepecus Cocco, 1829: 146 (type species: *Argyrolepecus hemigymnus* Cocco, 1829, by monotypy).

Pleurothysis Lowe, 1843: 64 (type species: *Sternoptyx olfersi* Cuvier, 1843, by original designation).

Sternoptychides Ogilby, 1888: 1313 (type species: *Sternoptychides amabilis* Ogilby, 1888, by monotypy).

Diagnosis. Twelve abdominal, six supra-abdominal and two suprapectoral photophores; eyes telescopic, dorsally oriented; frontal ridges compressed dorsally above eyes; basisphenoid absent; several teeth directed anteriorly on posterior maxillary margin; dorsal "blade" consisting of several broadened pterygiophores anterior to dorsal rays; seven enlarged pleural ribs.

Description. Photophores: PO 1; PTO 1; BR 6; I 6; AB 12; PRO 1; SO 1; SP 2; SAB

6; PAN 4; AN 6; SC 4 (for anatomical details see Brauer, 1908; Bassot, 1966).

Spines: Post-temporals extended posteriorly to form a small spine; preopercle bears one ventrally and one posteriorly directed spine; retroarticular bears ventrally directed spine; basipterygia extended ventrally bearing one or two postabdominal spines; cleithrum extends ventrally forming preabdominal spine; spiny scales present in adults of some species below subcaudal and preanal photophores.

Eyes: Large, well developed, telescopic, lens dorsally oriented, fitting into dorsal grooves in the frontal bone.

Gill Rakers: Total 15–24; rakers well developed with rough toothlike surface; epi- and ceratobranchials bear well-developed spines on internal surface.

Jaws and Dentition: Jaws somewhat vertically oriented; premaxilla well developed, toothed, and major upper jaw bone in gape; maxilla also somewhat in-

cluded in gape, toothed, the posteriormost teeth curved markedly forward; lower jaw sturdy, heavily toothed, occasionally with large canines; dentition consisting of multi-rowed single cusped, curved caninellike teeth; palatine teeth present, often well developed; epibranchial of third and fourth arch extends ventrally and laterally to form toothed plates.

Meristics: Vertebrae 35-40; C. 9+10; D. 8-10; A. 6-8 + 5-6.

Color: Bright silvery in life, quickly lost in formalin preservative; dark pigmentation often striated posteriorly; stable for long periods in preservation.

Internal Anatomy: Relatively thin-walled swim bladder (see Marshall, 1960) and gas gland well developed; digestive tract simple, consisting of heavily pigmented, double compartmented stomach; the anterior internal lining very thick walled and covered with rasping tubercles; posterior lining thin and distensible, five to seven thick-fingered pyloric caecae, large liver, and a short straight intestine; caelomic cavity lined with heavily pigmented membrane; gonads when mature fill the dorsal and lateral posterior half of the body cavity; nephritic tissue moderately well developed.

Species complexes. There has been substantial radiation within the genus and even to some extent within the species complexes. The *A. affinis* complex appears to be the most primitive and other forms can be derived from it. Primitive characters of this complex include: three hypural elements in lower caudal lobe; posterior ventral photophores in an almost unbroken series; glandular photophore ar-

rangement simple, the posterior photophores not joined in glandular clusters; little reinforcement of posteriormost pleural rib; body not markedly deepened anteriorly; basipterygia lacking support arm for keel plates; generally unspecialized axial skeleton, including lack of marked broadening of anterior haemal spines; vertebral number 38-40.

The more advanced members of the genus are characterized by two hypural elements in the lower caudal lobe; posterior photophores joined into distinct glandular clusters; a general deepening of the anterior body region with subsequent reduction in vertebral number; increased complexity of structural ossification especially in the axial skeleton, including a marked reinforcement of the last large pleural rib, and a keel supporting extension on the left basipterygia.

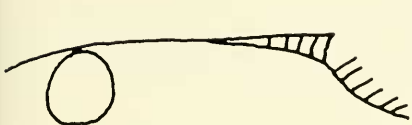
A. hemigymnus appears slightly more primitive than the *A. lychnus* complex and is highly specialized. Important characters include: primitive transitional vertebrae (like *A. affinis*); dwarfism (maximum length 38-40 mm); fused basipterygia forming single postabdominal spine; 38 vertebrae; epitotics with dorsal extensions (Fig. 7); peculiar dorsal blade shape, often with supplementary spiny spurs on the major element.

The most specious group, the *A. lychnus* complex, shows a high degree of structural ossification in the axial skeleton, including the dorsal and anal pterygiophore systems; some species have developed long, fang-like canines in the lower jaw; there is a marked deepening of the anterior body region with reduction in vertebral number.

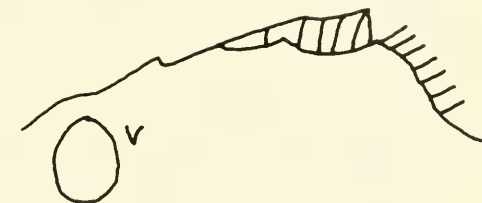
KEY TO THE SPECIES OF *Argyrolepecus*

- 1a. Supra-abdominal, preanal, anal, and subcaudal photophores in a nearly continuous straight line; subcaudal photophores separate, an appreciable gap between each photophore; 3 separate hypural elements in lower caudal lobe *A. affinis* complex 3
- b. Supra-abdominal, preanal, anal, and subcaudal photophores not in a continuous straight line; subcaudal photophore group in a single glandular cluster, no appreciable gap between each photophore; two separate hypural elements in lower caudal lobe 2
- 2a. A single posteriorly directed, serrate postabdominal spine; gap between anal and subcaudal photophore groups greater than 2.2 times gap between preanal and anal groups; dorsal rays 8 *A. hemigymnus* (p. 42).

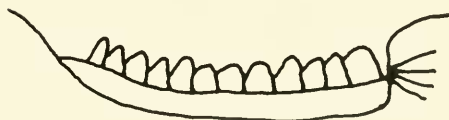
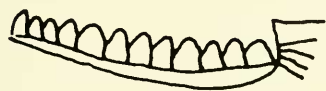
- b. Two separate postabdominal spines; anal subcaudal gap less than 2.0 times anal-pre-anal gap; dorsal rays 9 *A. lychnus* complex 4
- 3a. Dorsal blade low, its height less than one-third its length; body margin not markedly raised posterior to dorsal blade; ventral keel scales do not extend far below abdominal photophores; no laterally directed sphenotic spine near dorsal, posterior edge of orbit *A. affinis* (p. 34).
- b. Dorsal blade high, its height greater than one-third its length; body margin markedly raised posterior to dorsal blade; ventral keel scales extend well below abdominal photophores forming flaplike process; prominent laterally directed sphenotic spine near dorsal, posterior edge of orbit *A. gigas* (p. 38).



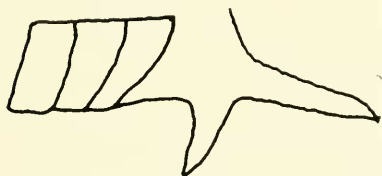
a.



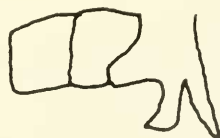
b.



- 4a. Posterior postabdominal spine directed posteroventrally and markedly larger than the anterior; anterior margin of posteriormost abdominal keel scale slants markedly forward; standard length less than 3.4 times body depth; pair of enlarged canine teeth present in lower jaw; subcaudal spines present *A. aculeatus* (p. 48).
- b. Both postabdominal spines of about equal length and size; anterior margin of posteriormost abdominal keel scale almost vertical; SL greater than 3.5 times body depth; pair of enlarged canines may or may not be present in lower jaw; subcaudal spines may or may not be present 5

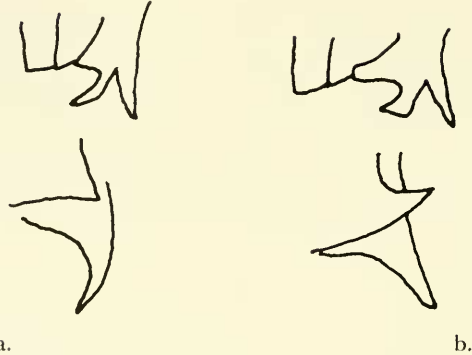


a.

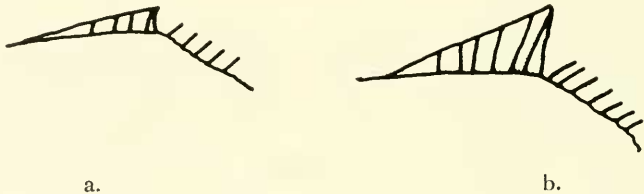


b.

- 5a. Pair of enlarged canine teeth in lower jaw; sharply pointed anteriormost postabdominal spine curved markedly and evenly forward; upper preopercular spine short, not extending much beyond posterior border of preopercle; outermost tips of dorsal and ventral-most caudal rays streaked with dark pigment (fish greater than 35 mm) *A. olfersi* (p. 52).
- b. No pair of enlarged canines in lower jaw; anteriormost postabdominal spine squared or blunt (except very small individuals), not curving evenly forward; upper preopercular spine extends well beyond posterior border of preopercle; no pigment on outermost caudal rays 6



- 6a. Dorsal blade low, blade height less than 2.5 mm for SL 25–50 mm, less than 3.1 mm for SL 50–70 mm; body narrow (see regression, body depth, Table 11); no spines on scales below subcaudal photophores; dark well-developed pigment spots form line along posterior midline (especially in smaller sizes); upper preopercle spine usually curved dorsally, never ventrally *A. sladeni* (p. 56).
- b. Dorsal blade high, blade height greater than 2.7 mm for SL 25–50 mm, greater than 3.8 mm for SL greater than 50 mm; body robust (see regression, body depth, Table 14); spiny scales present below subcaudal photophores (fish greater than 30 mm SL); pigment spots minute along posterior midline; upper preopercle spine usually curved ventrally, never dorsally *A. lychnus* (p. 63).



Argyropelecus affinis Garman Figure 19

Argyropelecus affinis Garman, 1899: 237 (holotype USNM 44593; tropical North Atlantic; not seen); Brauer, 1901: 120; 1906: 103 (fig. larvae); Regan, 1908: 218; Barnard, 1925: 153; Norman, 1930: 301 (fig.); Jespersen, 1934: 15 (fig.); Fowler, 1936: 221; Beebe, 1937: 201; Parr, 1937: 49; Norman, 1939: 19; Nybelin, 1948: 23; Misra, 1952: 367; Smith, 1953: 102; Haig, 1955: 321; Fowler, 1956: 67; Schultz, 1961: 597 (fig.); Bahamonde, 1963: 83; Blache, 1964: 71 (fig.); Schultz, 1964: 241 (fig.); Backus et al., 1965: 142; Bussing, 1965: 185; Bright and Paquegnat, 1969: 27.

Argyropelecus pacificus Schultz, 1961: 599 (fig.); 1964: 241; Berry and Perkins, 1965: 625; Lavenberg and Ebeling, 1967: 185.

Species distinction. Differs from *A. gigas*

(in addition to key characters) by its narrower body depth and trunk (see regression, body depth, Tables 2 and 3); less distinct trunk striations; relatively longer teeth in lower jaw; less well-developed post-temporal spines; smooth dorsal body surface; and less well-developed neurocranial crests (frontals, sphenotics, and parietals).

Description. D. 9; A. 12–13; P. (10) 11; total gill rakers 18–22; vertebrae 38–39 (40).

Medium size species rarely exceeding 70 mm SL; body more evenly tapered than others in genus; body depth at end of dorsal greater than 3.5 times into SL; caudal peduncle long and narrow, its depth

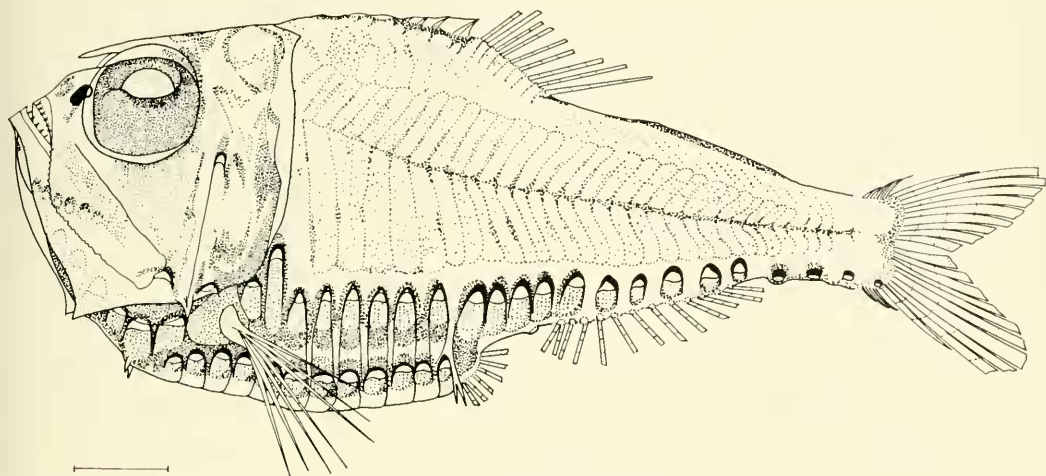


Figure 19. *Argyropelecus affinis*; R/V CHAIN, Cruise 60; Station 1257; SL 51 mm.

less than length of subcaudal photophore group; dorsal spine low, its height less than one-third its length; post-temporal spine short; postabdominal spines of equal size, with no marked curving; dorsal pre-

opercle spine directed latero-anteriorly; ventral preopercle spine long, curved anteriorly; jaws large; teeth short, recurved, better developed in lower jaw; gill rakers long, closely set; in preservative, trunk

TABLE 2. REGRESSION STATISTICS FOR VARIOUS POPULATIONS OF *A. AFFINIS*.

Character	Regression	
	A	B
<i>Indian Ocean</i> (5°–12°N, 160°–168°E)		
Body depth	-1.83	0.49 ± .146
Jaw length	-0.78	0.25 ± .065
		N = 11
<i>Gulf of Guinea</i>		
Body depth	-2.44	0.46 ± .121
Jaw length	-0.27	0.22 ± .060
Jaw width	-0.23	0.12 ± .059
		N = 10
<i>NW Atlantic</i> (30°–33°N, 73°–78°W)		
Body depth	2.59	0.37 ± .176
Jaw length	-0.78	0.24 ± .107
Jaw width	-1.35	0.14 ± .087
		N = 7
<i>SE Pacific</i> (Chile)		
Body depth	0.55	0.42 ± .086
Jaw length	0.64	0.21 ± .047
		N = 13
<i>NE Pacific</i> (California)		
Body depth	-1.02	0.49 ± .062
Jaw length	0.27	0.22 ± .029
		N = 19

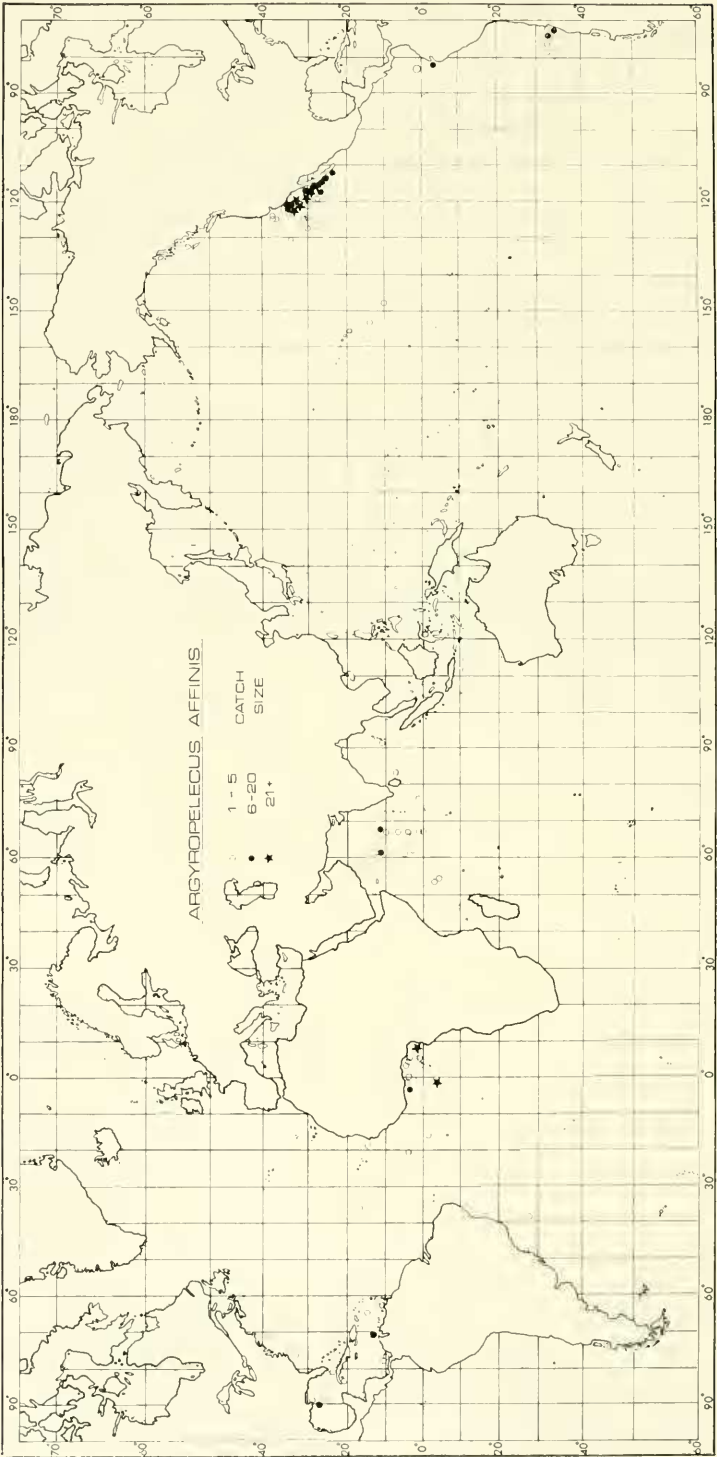


Figure 20. Horizontal distribution of *A. affinis*. Catch size categories refer to the number of individuals taken in that haul.

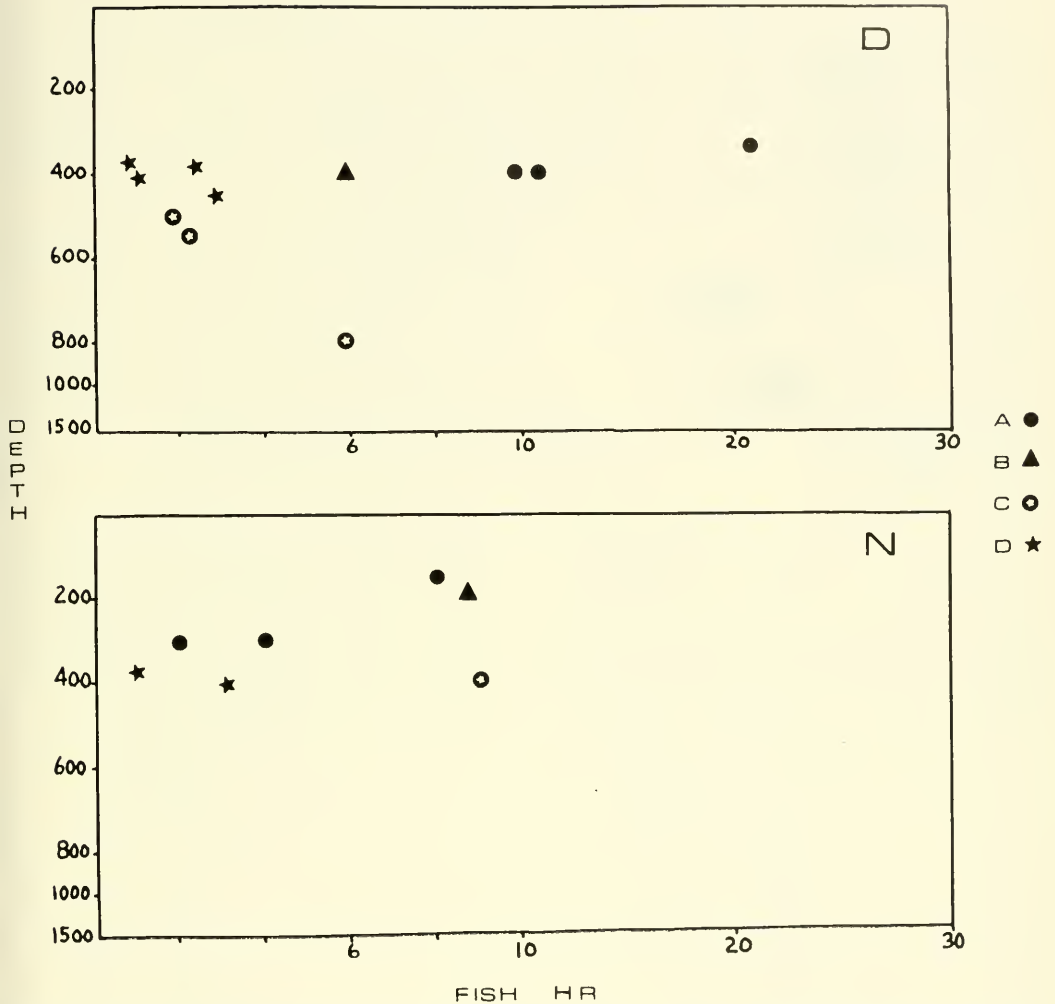


Figure 21. Diurnal vertical distribution of *A. affinis* determined by rate of capture with depth during the day (D) and night (N). A = Pacific (California); B = Pacific (Chile); C = Gulf of Guinea; D = Gulf of Mexico and Caribbean.

region exhibits cross pigment striations with well-defined, midlateral line.

Distribution. Horizontal distribution (Fig. 20): Taken abundantly in the Gulf of Guinea, off California, Chile, and in the northern Indian Ocean; moderate catches are recorded from the northern Gulf of Mexico and the coast of Venezuela in the Caribbean; smaller catches which may represent possible populations are recorded southeast of Hawaii, south of Java, and off the southeast coast of the United States;

scattered samples representing this species appear in the Bay of Bengal, Gulf of Aden, tropical Atlantic, and off the southeast coast of Brazil. (Additional records: Atlantic, occasional catches between Azores and Madeira; Pacific, moderate catches near coast of northern Peru.)

Vertical distribution (Fig. 21): Appears concentrated between 350 m and 600 m by day with the highest concentrations in the vicinity of 400 m; by night the distribution is somewhat more shallow, major

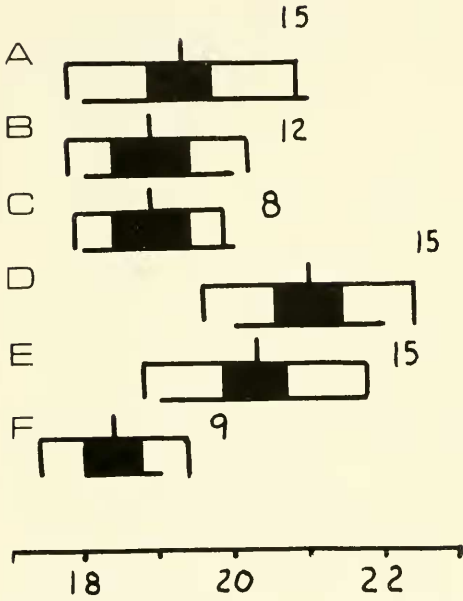


Figure 22. Geographic variation in gill raker number in *A. affinis*. A = Gulf of Guinea; B = Caribbean; C = Indian Ocean; D = Pacific (Chile); E = Pacific (California); F = NW Atlantic (NW Atlantic packet). Numbers refer to sample size.

concentrations occurring from 170 m to 400 m. With the possible exception of the Gulf of Guinea, there are no indications of marked geographic variation in depth distribution, although Appendix C indicates slightly shallower daytime depths off California than in the tropical Atlantic.

Geographic variation. Five separate populations could be recognized and are identified and statistically defined in Figures 22 and 23 and Table 2. Regression sample sizes are small in the Atlantic. Figure 23 indicates positional variation in body depth even though there is no significant difference in slope.

Argyrolepecus gigas Norman
Figure 24

Argyrolepecus gigas Norman, 1930: 302 (holotype BMNH 1.12.329; Gulf of Guinea; not seen); Jespersen, 1934: 15 (fig.); Fowler, 1936: 1208; Parr, 1937: 49; Maul, 1949a: 17 (fig.); 1949b: 13; Koefoed, 1961: 3; Schultz, 1961: 600 (fig.); 1964: 241 (fig.); Blache, 1964: 71 (fig.); Backus et al., 1965: 129; Bright and Paquegnat, 1969: 28.

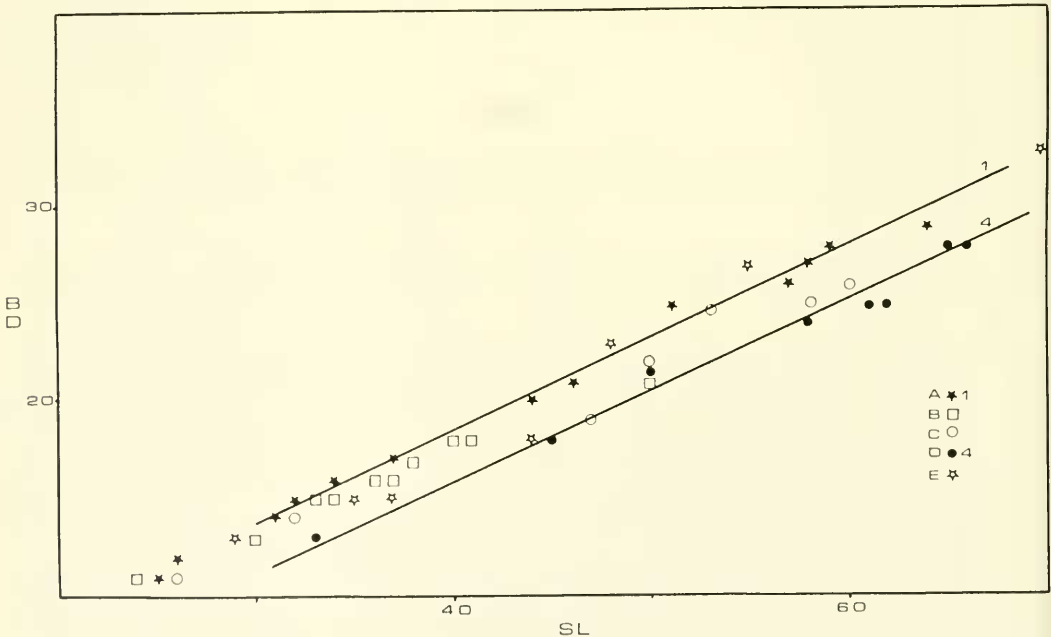


Figure 23. Geographic variation in the regression of body depth (BD) on standard length (SL) in *A. affinis*. A = Pacific (California); B = Pacific (Chile); C = NW Atlantic; D = Gulf of Guinea; E = Indian Ocean.

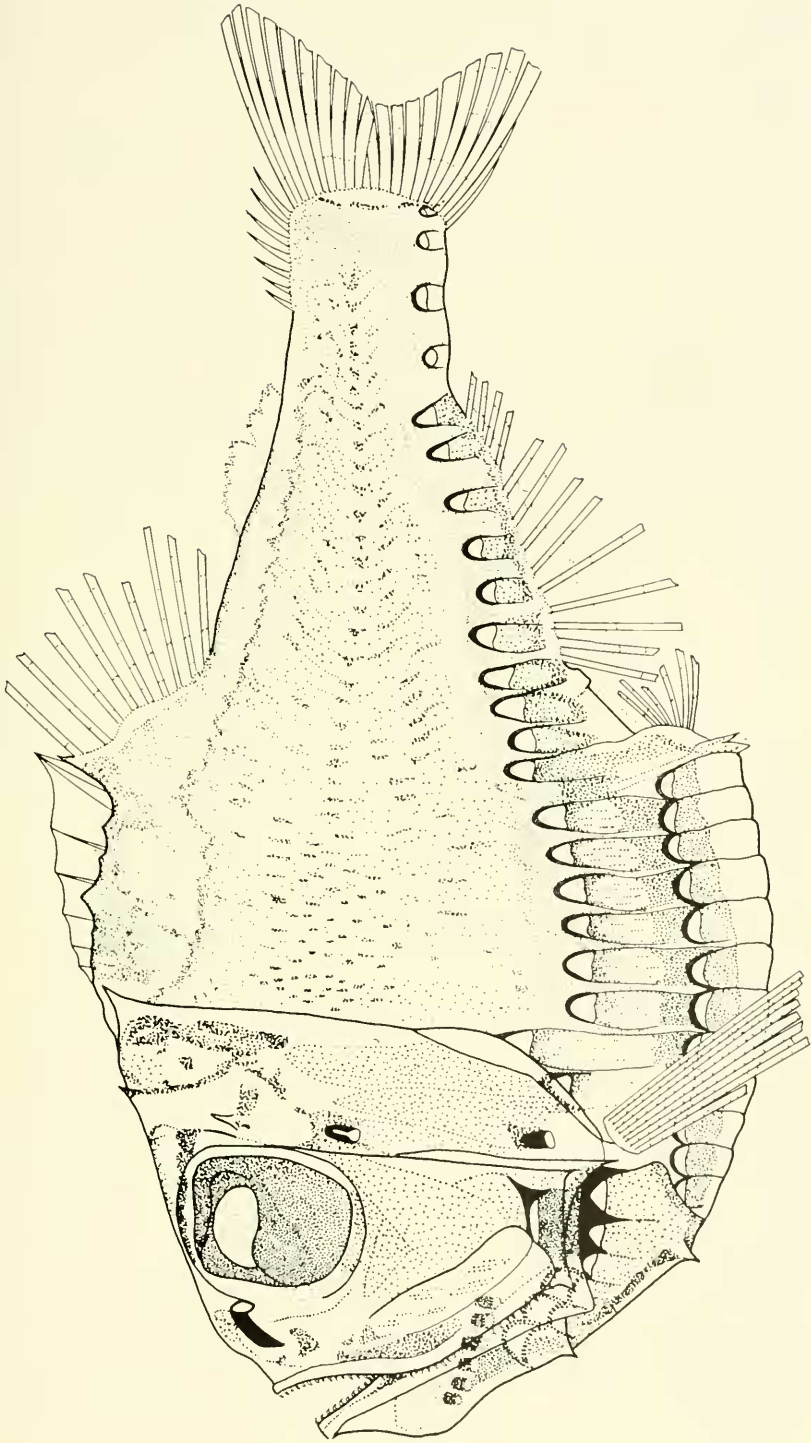


Figure 24. *Argyropelecus gigas*; R/V CHAIN, Cruise 60; Station 1308; SL 52 mm.

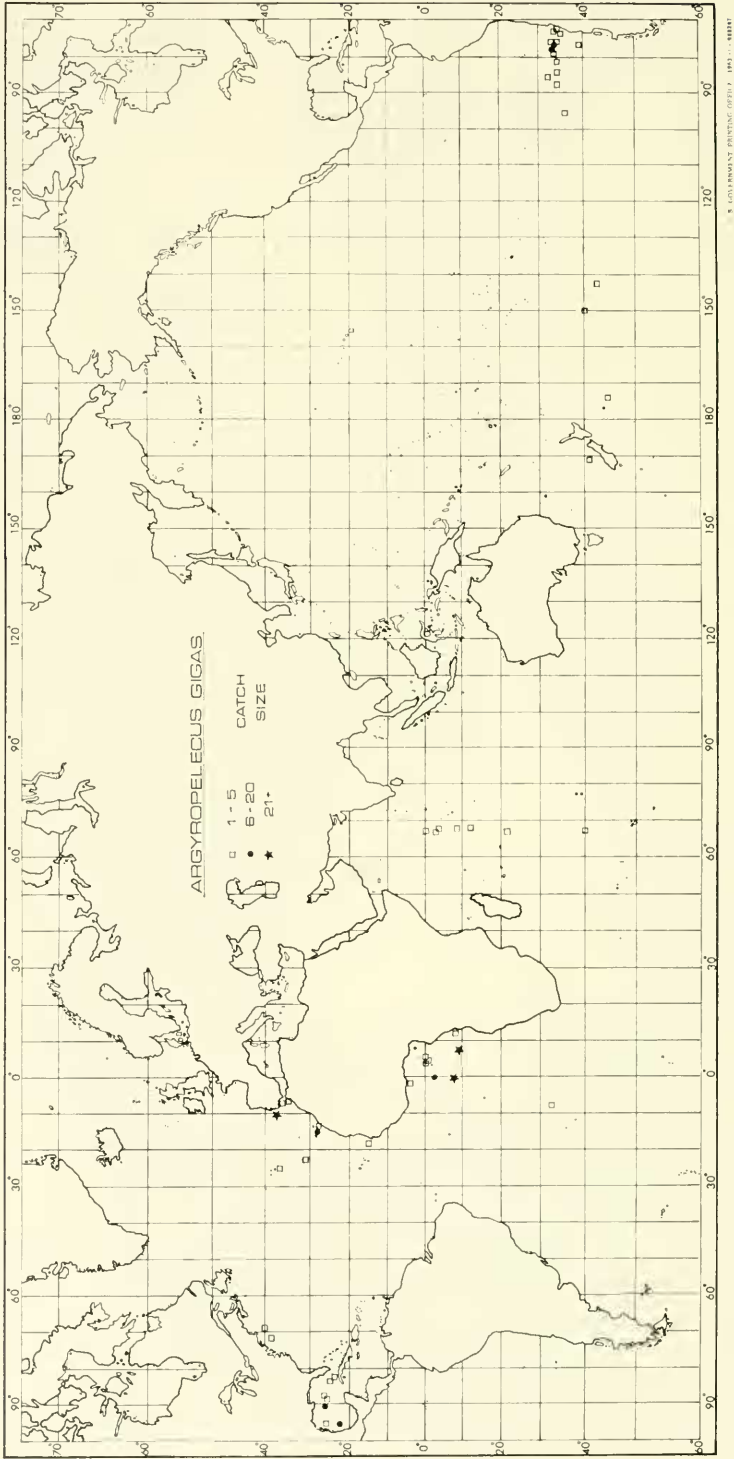


Figure 25. Horizontal distribution of *A. gigas*. Catch size categories refer to the number of individuals taken in that haul.

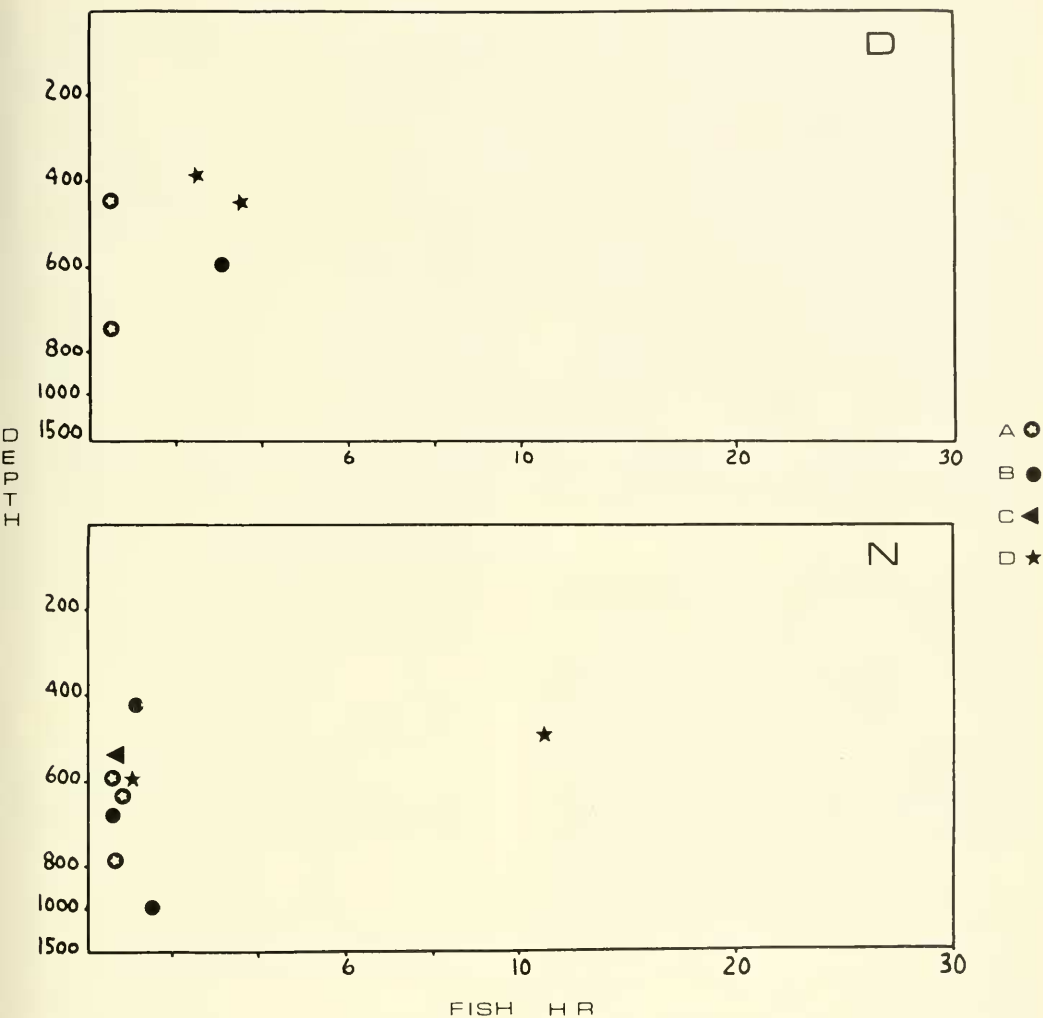


Figure 26. Diurnal vertical distribution of *A. gigas* determined by rate of capture with depth during the day (D) and night (N). A = Pacific (Chile); B = Gulf of Guinea; C = Gulf of Mexico; D = NE Atlantic.

Argyrolepecus affinis: Jespersen, 1915: 6; Roule and Angel, 1933: 46; Buen, 1935: 52; Nybelin, 1948: 23; Dollfus, 1955: 1.

Species distinction. See *A. affinis* (p. 34).

Description. D. 9 (10); A. 12–13; P. 10–11; total gill rakers 18–21; vertebrae 38–39.

Giant species often exceeding 110 mm SL; trunk triangulate, body depth at end of dorsal less than 3.3 times into SL; caudal

peduncle deep, its depth nearly equal to subcaudal photophore length; dorsal spine high, its height greater than one-third its length; post-temporal spine prominent; postabdominal spines symmetrical; preopercle spines as in *A. affinis*; jaws large; teeth small, recurved, a pair of larger canine teeth in upper jaw (premaxilla); gill rakers well developed; parietals, post-temporal, frontals and sphenotics with prominent spines or flanges; in preserva-

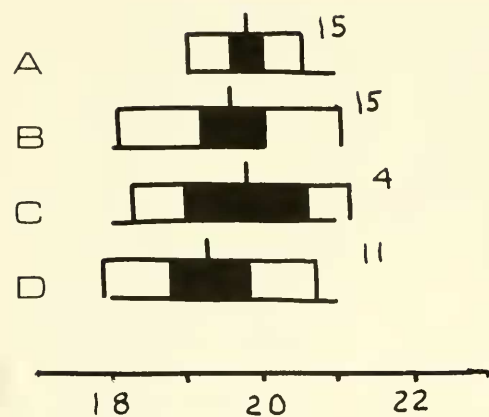


Figure 27. Geographic variation in gill raker number in *A. gigas*. A = NE Atlantic; B = Gulf of Guinea; C = Indian Ocean; D = Pacific (Chile). Numbers refer to sample size.

tive pigment in small spots along midline; very heavy mucoid secretion often present.

Distribution. Horizontal distribution (Fig. 25): Although occurring in all oceans except the North Pacific, this species appears quite restricted locally. It is taken in abundance in the Gulf of Guinea, in the eastern North Atlantic off North Africa and southern Spain, in the northern Gulf

of Mexico, and off Chile in the South Pacific; small catches of this species are recorded along longitude 67°E from the equator to 40°S in the Indian Ocean, across the South Pacific between 35°S and 50°S from Chile to New Zealand in the South Pacific, and between New York and Cape Cod in the North Atlantic. Additional records: 36°35'S, 95°28'E.

Vertical distribution (Fig. 26): Concentrated between 400 m and 600 m; no indication of diurnal vertical movement or marked geographic variation in depth distribution.

Geographic variation. While having the most disjunct horizontal distribution in the family, this species shows the least variability in the characters measured (Fig. 27, Table 3). Sample sizes in most cases were quite small, and increased sampling and the use of other characters may result in better population definition.

Argyropelecus hemigymnus Cocco
Figure 28

Argyropelecus hemigymnus Cocco, 1829: 146 (holotype unknown; Mediterranean, Messina); Alcock, 1896: 331; Jordan and Evermann, 1896:

TABLE 3. REGRESSION STATISTICS FOR VARIOUS POPULATIONS OF *A. GIGAS*.

Character	Regression	
	A	B
<i>Gulf of Guinea</i>		
Body depth	0.65	0.50 ± .131
Jaw length	0.71	0.21 ± .055
Jaw width	-0.33	0.14 ± .040
		N = 10
<i>NE Atlantic</i> (37°N, 10°W)		
Body depth	-4.42	0.58 ± .104
Jaw length	0.23	0.22 ± .044
Jaw width	-1.36	0.16 ± .029
		N = 14
<i>Indian Ocean</i> (0°-40°S, 167°E)		
Body depth	-0.60	0.54 ± .332
Jaw length	0.39	0.22 ± .137
		N = 5
<i>SE Pacific</i> (Chile)		
Body depth	-2.21	0.54 ± .155
Jaw length	-0.71	0.24 ± .068
		N = 9

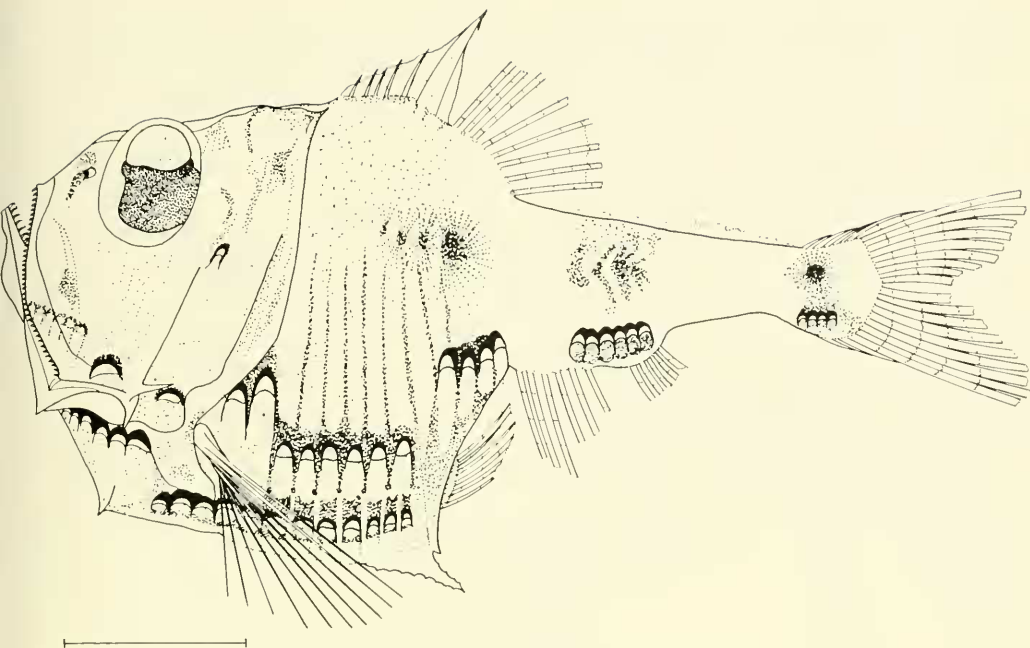


Figure 28. *Argyropelecus hemigymnus*; R/V CHAIN, Cruise 60; Station 1299; SL 30 mm.

604; Handrick, 1901: 1 (anatomy, nervous system, light organs); Collett, 1903: 108; Ledenfeld, 1905: 170 (light organs); Braner, 1906: 106 (larvae, fig.); Regan, 1908: 218; Ehrenbaum, 1909: 357 (larvae, fig.); Zugmayer, 1911: 52; Holt and Byrne, 1913: 21 (larvae, fig.); Jespersen, 1915: 6; Jespersen and Tåning, 1919: 220 (larvae, eye muscles); Nusbaum-Hilarowicz, 1923: 10 (anatomy); Barnard, 1925: 153; Jespersen and Tåning, 1926: 59; Sanzo, 1928: 50 (eggs, larvae); Norman, 1930: 301; Borodin, 1931: 44 (eggs, larvae); Jespersen, 1934: 15 (larvae, fig.); Buen, 1935: 52; Fowler, 1936: 1208; Beebe, 1937: 201; Parr, 1937: 49 (spines); Norman, 1937: 82; 1939: 19; Nybelin, 1948: 23; Maul, 1949b: 13; Misra, 1952: 367; Smith, 1953: 102; Kotthaus and Krefft, 1957: 3; Perès, 1958: 4 (bathyscaphe); Koefoed, 1961: 5; Schultz, 1961: 601; 1964: 241; Blache, 1964: 71; Backus et al., 1965: 139; Kotthaus, 1967: 22 (photo, otoliths); Bright and Paquegnat, 1969: 28.

Argyropelecus d'urvillei Valenciennes, in Cuvier and Valenciennes, 1849: 405; Goode and Bean, 1896: 127.

Argyropelecus intermedius Clarke, 1878: 248; Schultz, 1961: 587; 1964: 241; Blache, 1964: 71; Berry and Perkins, 1965: 625; Kotthaus, 1967: 11 (photo.); Lavenberg and Ebeling, 1967: 185.

Argyropelecus heathi Gilbert, 1905: 601; Fowler, 1949: 42; Haig, 1955: 321.

Species distinction. Differs from all other species in genus by its narrow trunk, single postabdominal spine, small size, minute teeth, presence of only eight dorsal and eleven anal rays.

Description. D. 8; A. 11; P. 10–11; total gill rakers (18) 19–23 (24); vertebrae (36) 37–38.

Dwarf species rarely exceeding 38 mm SL; trunk very long and narrow; its depth at origin of anal photophores three or more times into greatest body depth, subcaudal photophores well separated from anals; dorsal spine medium-to-high, its height often exceeds its length; post-temporal spines well developed; postabdominal spines fused to form a single spine complex; lower preopercle spine directed ventrally, the upper postero-dorsally; jaws medium; teeth small to minute; gill rakers long and numerous; in preservative abdominal region dark, trunk pigmentless

TABLE 4. COMPARISONS OF REGRESSION STATISTICS FOR THREE POPULATIONS OF *A. HEMIGYMNUS*. REGRESSION A REFERS TO PIGMENT FORM A (SEE TEXT); REGRESSION B REFERS TO PIGMENT FORM B. NS INDICATES NO SIGNIFICANT DIFFERENCE BETWEEN THE SLOPES OF THE TWO REGRESSIONS INDICATED.

Character	Regression A		Regression B		Slope-T-Test
	A	B	A	B	
<i>Southern Ocean</i> (Pacific)					
Body depth	-0.61	0.53 \pm .041	0.45	0.48 \pm .063	NS
Caudal peduncle width	0.52	0.07 \pm .099	0.59	0.07 \pm .016	NS
Jaw length	0.09	0.23 \pm .026	0.68	0.21 \pm .036	NS
Jaw width	-0.36	0.14 \pm .020	0.01	0.13 \pm .041	NS
	N = 41		N = 49		
<i>Gulf of Mexico</i>					
Body depth	-0.95	0.54 \pm .086	1.62	0.45 \pm .161	NS
Caudal peduncle width	0.30	0.09 \pm .020	0.34	0.09 \pm .037	NS
Jaw length	0.15	0.23 \pm .050	-0.15	0.26 \pm .108	NS
Jaw width	-0.33	0.14 \pm .038	0.88	0.09 \pm .053	NS
	N = 17		N = 10		
<i>N Pacific</i> (California)					
Body depth	0.38	0.51 \pm .121	0.43	0.49 \pm .176	NS
Dorsal blade	0.56	0.08 \pm .031	0.72	0.07 \pm .063	NS
Jaw length	0.60	0.21 \pm .047	-0.58	0.24 \pm .103	NS
Jaw width	0.30	0.11 \pm .042	-0.36	0.14 \pm .060	NS
	N = 14		N = 8		

except in definite patches along midline and above anal and subcaudal photophore groups.

Pigment forms. Two pigment forms designated form "A" and form "B" occur over much of the species range. Form A is characterized by distinct and clearly defined body pigmentation, while in form B the body pigmentation is quite diffuse. This pigment difference is not a function

of size or sex, is intermediate in few individuals, and both forms do occur in the same catch. A morphometric analysis of three sympatric populations in several characters and meristics (Table 4; Figs. 33 and 34), plus measurements from one or the other pigment forms from other areas (Table 6) failed to show any significant difference between sympatric populations. In addition, there was no

TABLE 5. DIURNAL CAPTURE COMPARISONS OF THE TWO PIGMENT FORMS OF *A. HEMIGYMNUS* FROM VARIOUS AREAS FROM DEPTHS OF 0 M TO 1000 M. # = TOTAL NUMBER OF HAULS; # POS. = NUMBER OF POSITIVE HAULS; # 20+ = NUMBER OF POSITIVE HAULS CONTAINING 20 OR MORE INDIVIDUALS.

Locale	Pigment Form	Night			Day		
		#	# pos.	# 20+	#	# pos.	# 20+
NE Atlantic (20-35°N, 0-30°W)	A	41	9	2	47	20	14
	B	41	25	9	47	7	1
N Atlantic (37-45°N, 30-70°W)	A	129	15	6	102	43	22
	B	129	27	12	102	6	2
Gulf of Mexico and Caribbean	A	45*	3	1	35	19	6
	B	45*	4	0	35	0	0
Southern Ocean	A	58	12	3	25	19	3
	B	58	32	10	25	3	1

* 18 of these hauls were less than 200 m.

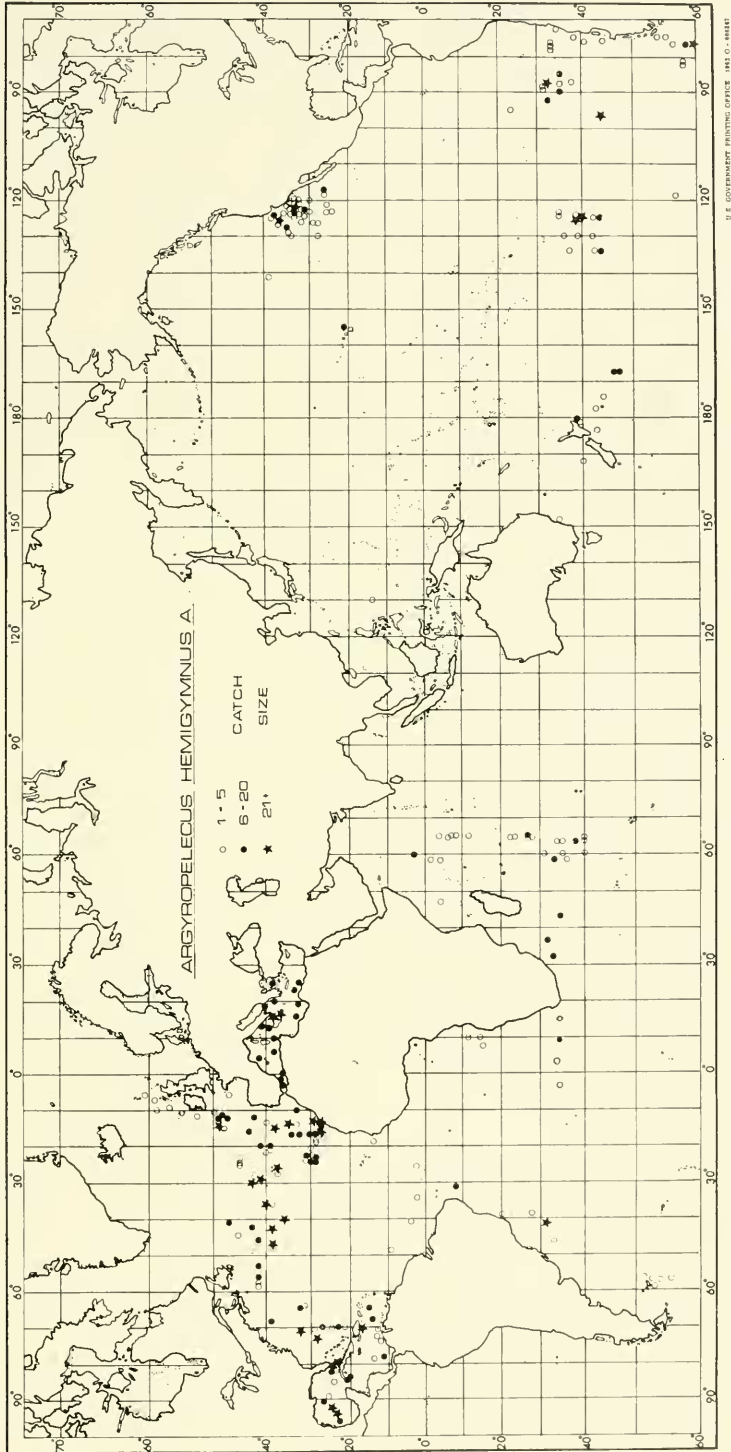


Figure 29. Horizontal distribution of *A. hemigymnus*, pigment form A. Catch size categories refer to the number of individuals taken in that haul.

consistent sorting out over the range of variability of any one form in any character. Analysis of diurnal depth distributions revealed a marked sorting out of pigment types with form A most numerous during the day while form B was predominantly caught at night (Table 5). Distributions from which Table 5 was compiled were chosen from areas where this species appears to occur throughout the horizontal sampling space. It is concluded that these two forms represent pigment states of the same species whose states can be varied individually.

Recently Badcock (1969) reported diel color variation in several mesopelagic fishes (including *A. hemigymnus*) and attributed it to a correlation with ambient light conditions. This appears to be the case in *Argyropelecus hemigymnus*. There are two anomalies, however, which raise some interesting points. First is the occurrence, occasionally in great numbers, of the day form at night and the night form during the day. Second is the relatively rare occurrence of form B in the tropics and its apparent absence from the Mediterranean (over 300 specimens examined).

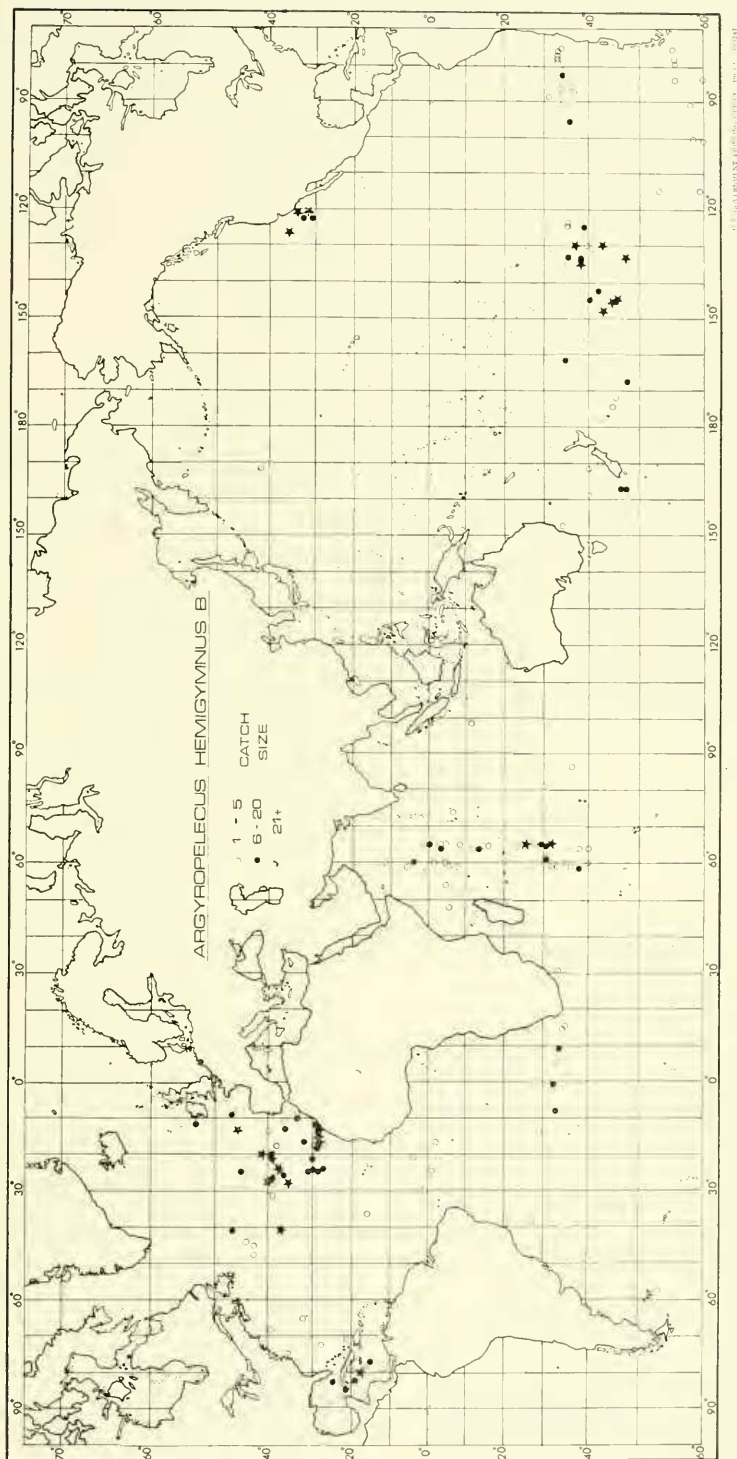
Tropical submergence is present in this species (see below) and may help explain the rareness of form B in the tropics. Nevertheless, there is considerable complexity in the depth distribution of this species and if the pigment change is sensitive to small differences in ambient light, it may be used as an indication of seasonal or geographical changes in depth distribution, changes in sea water turbidity, or of other correlated information.

Distribution. Horizontal distribution (Figs. 29 and 30): Occurs in the South Atlantic around the Falkland Islands and abundantly off the southeast coast of Brazil; a scattering of catches along latitude 35°S to the Cape of Good Hope suggests a broad distribution across the South Atlantic; occurs in small catches along the southwest African coast, appears absent in the Gulf of Guinea, but occurs in the

western tropical Atlantic; is taken in moderate numbers in the Caribbean and Gulf of Mexico and abundantly in the western Atlantic; is abundant across the North Atlantic and the eastern North Atlantic as far south as the Cape Verdes Islands; it represents the only species of this family in the Mediterranean, where it occurs abundantly in the western basin; scattered moderate-to-small catches are present from 5°N to 12°S latitude in the central Indian Ocean, and another population is scattered from 20°S to 40°S with several small catches reported from the southeastern and southwestern Indian Ocean; a single catch off the Philippines, another at 42°N, 169°E, and small catches from the Banda Sea and near Hawaii represent this species in the west and central Pacific; large populations occur off California and Chile; it is taken abundantly across the Southern Ocean from 35°–55°S latitude from Chile to New Zealand; taken in small numbers in the Tasman Sea and off Sidney, Australia.

Vertical distribution (Figs. 31 and 32): Occurs from 200 m to 700 m by day with the greatest concentration between 350–550 m; occurs from 100 m to 650 m by night with concentrations between 150–380 m; tropical submergence indicated in the Gulf and Caribbean by examining number of catches above 200 m (Appendix B) compared with the North Atlantic; by day it appears to concentrate at about 550 m in the Sargasso Sea (Dr. James Craddock, WHOI, personal conversation).

Geographic variation. At least seven different populations could be discerned and are identified and statistically defined for a number of characters in Tables 4 and 6 and Figures 33 and 34. Small samples from the central Pacific and Cape Verdes Islands may indicate separate populations also. Broad variations in slope between several populations were noted and these were tested for statistical significance (Table 7) indicating considerable worldwide variability and distinct population

Figure 30. Horizontal distribution of *A. hemigymnus*, pigment form B.

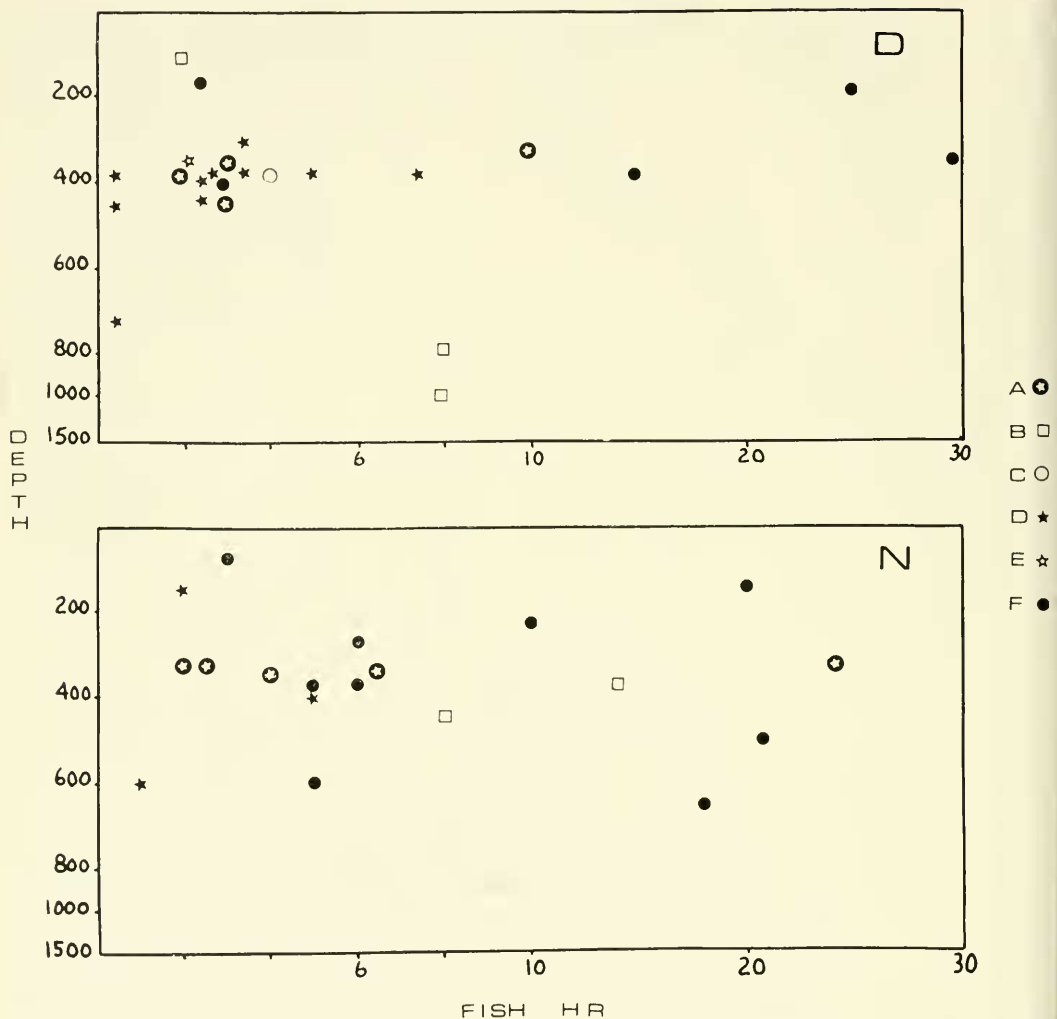


Figure 31. Diurnal vertical distribution of *A. hemigymnus*, pigment form A, determined by rate of capture with depth during the day (D) and night (N). A = Pacific (California); B = Southern Ocean; C = SW Atlantic; D = Gulf of Mexico and Caribbean; E = N Atlantic; F = NE Atlantic.

characteristics; dorsal blade height and gill raker number differences (Figs. 33 and 34) further emphasized the distinctness of populations in this species.

Argyrolepecus aculeatus Valenciennes Figure 35

Argyrolepecus aculeatus Valenciennes, in Cuvier and Valenciennes, 1849: 406 (holotype MNHNP 1817; Azores; not seen); Günther, 1864: 384; Sauvage, 1891: 483; Collett, 1903:

108; Brauer, 1906: 110; Regan, 1908: 218; Jespersen, 1915: 11; Norman, 1930: 301; Borodin, 1931: 68; Jespersen, 1934: 15; Beebe, 1937: 201; Bertin, 1940: 314 (holotype); Maul, 1949a: 17; Misra, 1952: 367; Bigelow and Schroeder, 1953: 149; Koefoed, 1961: 7; Schultz, 1961: 607; 1964: 241; Backus et al., 1965: 139; Kamohara and Yamakawa, 1965: 22; Bright and Paquegnat, 1969: 29.

Argyrolepecus olfersi: Goode and Bean, 1896: 127; Jordan and Evermann, 1896: 604 (?); Rivero, 1934: 31; 1936: 56; Cervigón, 1964: 1. *Argyrolepecus* (*Sternoptychides*) *amabilis* Ogilby.

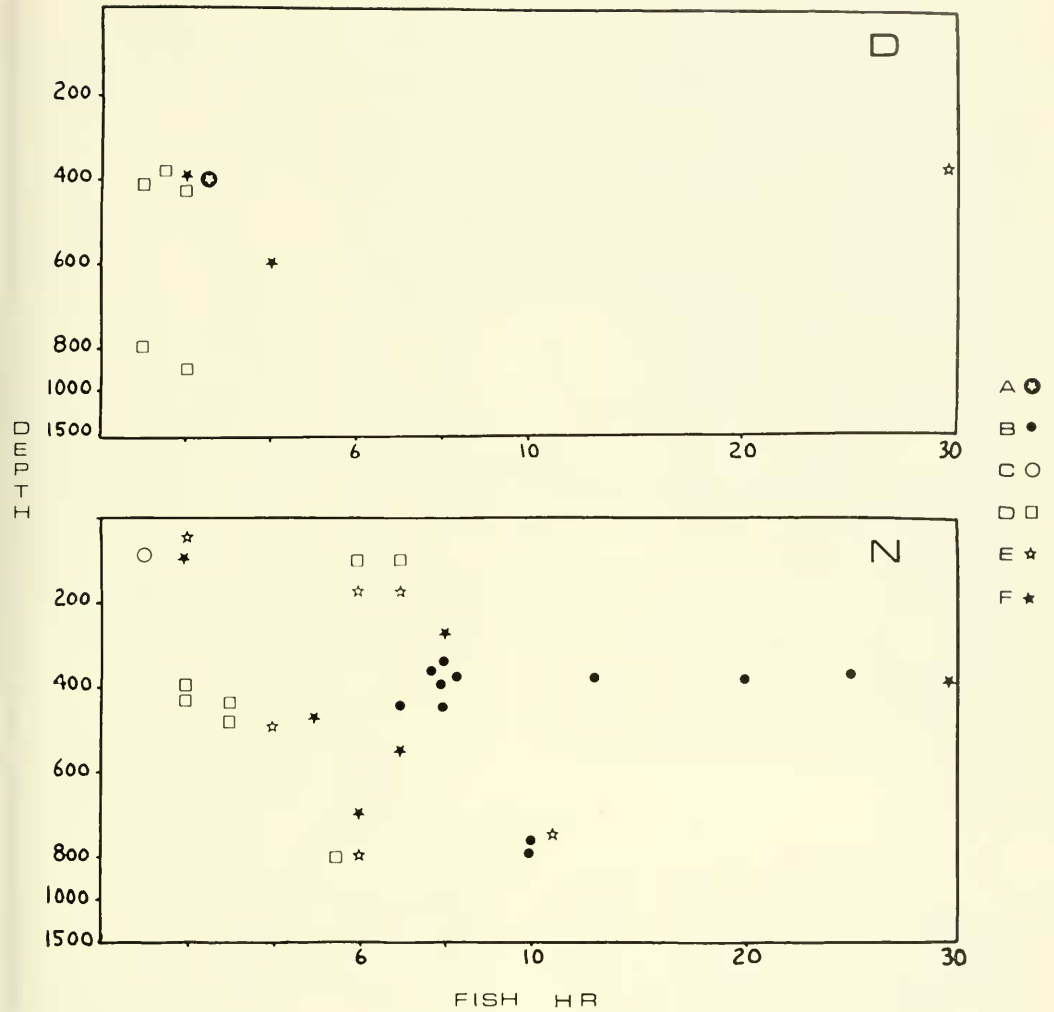


Figure 32. Diurnal vertical distribution of *A. hemigymnus*, pigment form B (see Fig. 31).

1888: 313; Goode and Bean, 1896: 127; McCulloch, 1923: 118; Whitley, 1940: 404; Koefoed, 1961: 7; Schultz, 1961: 607, 1964: 241. *Argyropelecus caninus* Garman, 1899: 235. *Argyropelecus acanthurus* (not Cocco) Fowler, 1936: 246; Maul, 1949b: 13; Dollfus, 1955: 24. *Argyropelecus micracanthus* Parr, 1937: 49. *Argyropelecus antrorsospinus* Schultz, 1937: 5.

Species distinction. See *A. olfersi* (p. 52).

Description. D. 9; A. 12; P. 10–11; total gill rakers 15–17; vertebrae 34–36.

Large species often exceeding 70 mm SL; body very deep, depth at end of

dorsal less than 1.4 into SL; dorsal spine quite high, its height about equal to its length; post-temporal spines present; dorsal surface of post-temporal with distinct serrations; postabdominal spines well developed, the posterior much larger than anterior; ventral keel extends well below body margin near postabdominal spines; preopercle spines short, both pointing ventrally; jaws large, teeth long, recurved, with two enlarged canines in lower jaw; spines present below and in front of subcaudal photophores; gill rakers medium to

TABLE 6. REGRESSION STATISTICS FOR VARIOUS POPULATIONS OF *A. HEMIGYMNUS*.

Character	Regression	
	A	B
<i>NE Atlantic</i> (36°–39°N, 27°W)		
Pigment Form B		
Body depth	1.44	0.45 ± .069
Caudal peduncle width	0.97	0.06 ± .016
Jaw length	1.69	0.17 ± .036
Jaw width	0.39	0.11 ± .035
		N = 35
<i>NW Atlantic</i> (36°N, 55–60°W)		
Pigment Form A		
Body depth	–0.33	0.51 ± .081
Caudal peduncle width	0.55	0.08 ± .019
Jaw length	–0.04	0.24 ± .052
Jaw width	0.43	0.12 ± .034
		N = 24
<i>Indian Ocean</i> (5°–35°S, 55°–65°E)		
Pigment Form B		
Body depth	–0.96	0.55 ± .266
Dorsal blade	0.35	0.11 ± .129
Jaw length	0.99	0.21 ± .158
Jaw width	0.83	0.09 ± .123
		N = 7
<i>Mediterranean</i>		
Pigment Form A		
Body depth	1.44	0.45 ± .104
Dorsal blade	–0.24	0.09 ± .030
Jaw length	1.16	0.20 ± .056
Jaw width	–1.38	0.19 ± .045
		N = 15

short, with dentate inner surfaces; pigment diffuse on trunk, no marked pigment on midline, pigment concentration above subcaudals present, pigmentless bar anterior to caudal peduncle in young.

Distribution. Horizontal distribution (Fig. 36): Taken abundantly in the Caribbean and Gulf of Mexico; in the western North Atlantic to about 40°N and 35°W; occurs in the northeastern Atlantic south

TABLE 7. SLOPE COMPARISONS OF REGRESSIONS OF SEVERAL CHARACTERS BETWEEN VARIOUS POPULATIONS OF *A. HEMIGYMNUS*. A = PIGMENT FORM A; B = PIGMENT FORM B.

Character	Population 1	Population 2	T	P
Jaw length	Gulf of Mexico B	NE Atlantic B	2.073	.05
	Gulf of Mexico A	NE Atlantic B	2.222	.035
	NW Atlantic A	NE Atlantic B	2.211	.034
	Southern Ocean A	NE Atlantic B	2.854	.005
Jaw width	Gulf of Mexico B	Southern Ocean A	2.109	.04
Caudal peduncle depth	Gulf of Mexico A	NE Atlantic B	2.659	.01
	Gulf of Mexico A	Southern Ocean A	2.098	.05
Jaw width	Mediterranean A	California A	2.548	.021

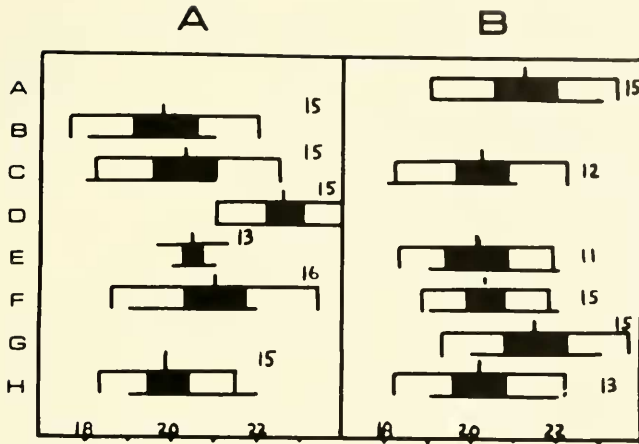


Figure 33. Geographic variation in gill raker number in *A. hemigymnus*, pigment forms A and B. A = NE Atlantic; B = NW Atlantic; C = Gulf of Mexico; D = Mediterranean; E = Indian Ocean; F = Southern Ocean (Pacific); G = N Pacific; H = Pacific (California). Numbers refer to sample size.

of about 35°N along the North African coast and associated islands; essentially absent from the tropical Atlantic; small to moderate catches in the southwestern Atlantic represent this species; taken in the central Indian Ocean from about 10°S to 40°S and reported abundant off the eastern South African coast; a few records scattered along the western Pacific from north of New Guinea to Japan represent it in the western Pacific; a number of moderate catches indicate its presence in the north central Pacific; these are matched by similar catches off Chile and one large haul off Sidney, Australia.

Vertical distribution (Fig. 37): Occurs between 200 m and 550 m by day with the greatest concentrations from 350–450 m; marked diurnal movement with major concentrations from 80–200 m at night; Sargasso Sea captures indicate concentrations at about 520 m by day (Dr. James Craddock, WHOI, personal conversation).

Geographic variation. Because of large samples available this species was used for a detailed population study in the Atlantic. It allowed checks to be made of within-population variation both from different years and as subsamples of the same catch; furthermore, an examination of samples

in the northwest Atlantic provided an opportunity to look at variations over at least 15° of longitude in the same biogeographic region. Table 8 records these results. In the northwest Atlantic, results indicate that population parameters remain constant in

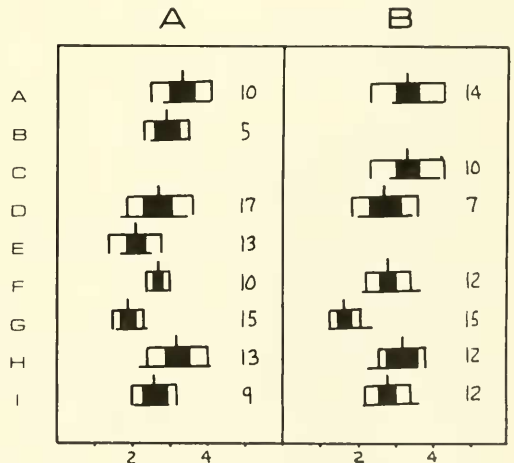


Figure 34. Geographic variation in dorsal blade height in *A. hemigymnus*, pigment forms A and B, for standard lengths 23–28 mm. A = NW Atlantic; B = Cape Verdes Islands; C = NE Atlantic; D = Gulf of Mexico; E = Mediterranean; F = Pacific (California); G = Southern Ocean; H = Indian Ocean; I = Caribbean and Tropical Atlantic. Numbers refer to sample size.

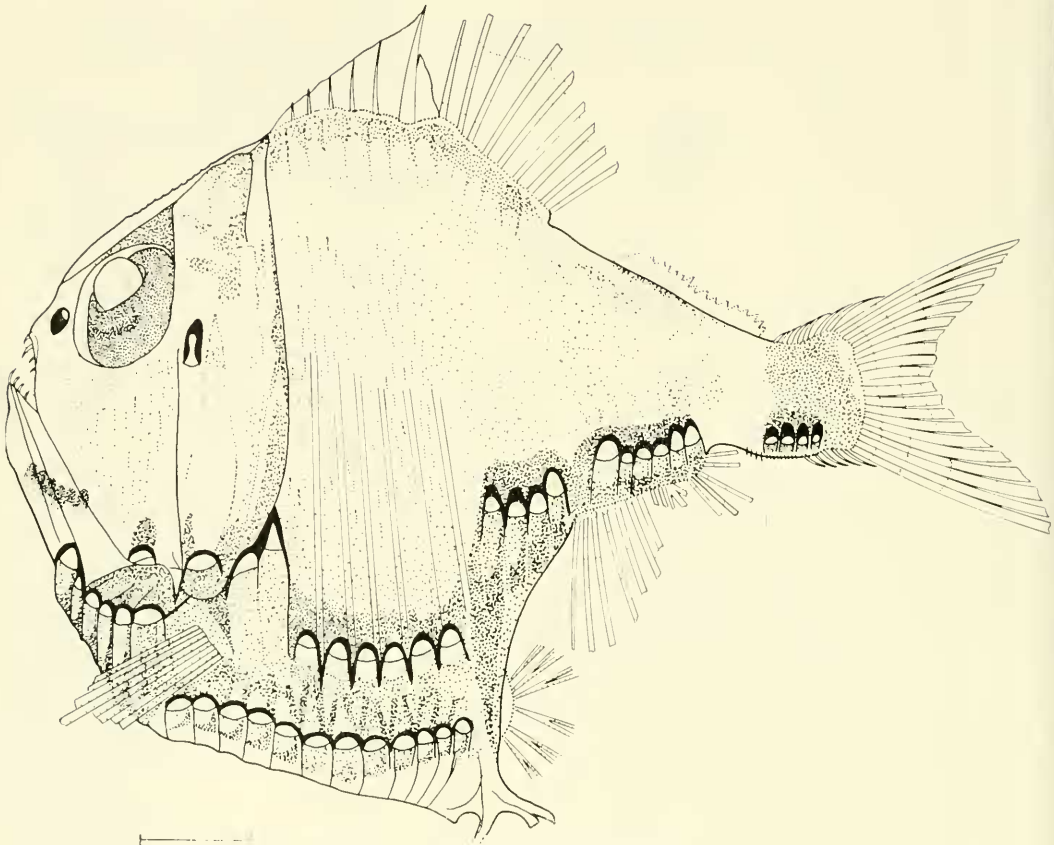


Figure 35. *Argyropelecus aculeatus*; R/V CHAIN, Cruise 60; Station 1266; SL 46 mm.

the same locality from year to year. In addition, populations in this area taken at the same latitude but separated by 15° of longitude show no indication of changes in values of parameters measured—in fact they appear to remain remarkably constant. Once again division of a large haul from the Caribbean into two subsamples gave little variability with adequate sample sizes. In a given area, populations seem to remain distinctive both from year to year and over a broad range in the same biogeographical region. There appears to be a clinal variation between populations in the Atlantic, going from the Caribbean, to the Gulf of Mexico, to the northwest Atlantic. Gill raker number and body

depth (Figs. 38 and 39) show a clinal variability and possibly jaw length (Table 8) as well. Six separate populations are identified and statistically defined in Table 8 and Figures 38 and 39. The South Pacific (Chile) population is quite distinct from the others. Differences in slope between the Caribbean and northeast Atlantic populations were significant in several characters (Table 9).

Argyropelecus olfersi (Cuvier)
Figure 40

Sternoptyx olfersi Cuvier, 1829: 316 (holotype MNHNP 1889; Cape of Good Hope; not seen).
Argyropelecus olfersi, Cuvier and Valenciennes, 1849: 408; Collett, 1903: 108; Brauer, 1906: 69; Regan, 1908: 218; Zugmayer, 1911: 52;

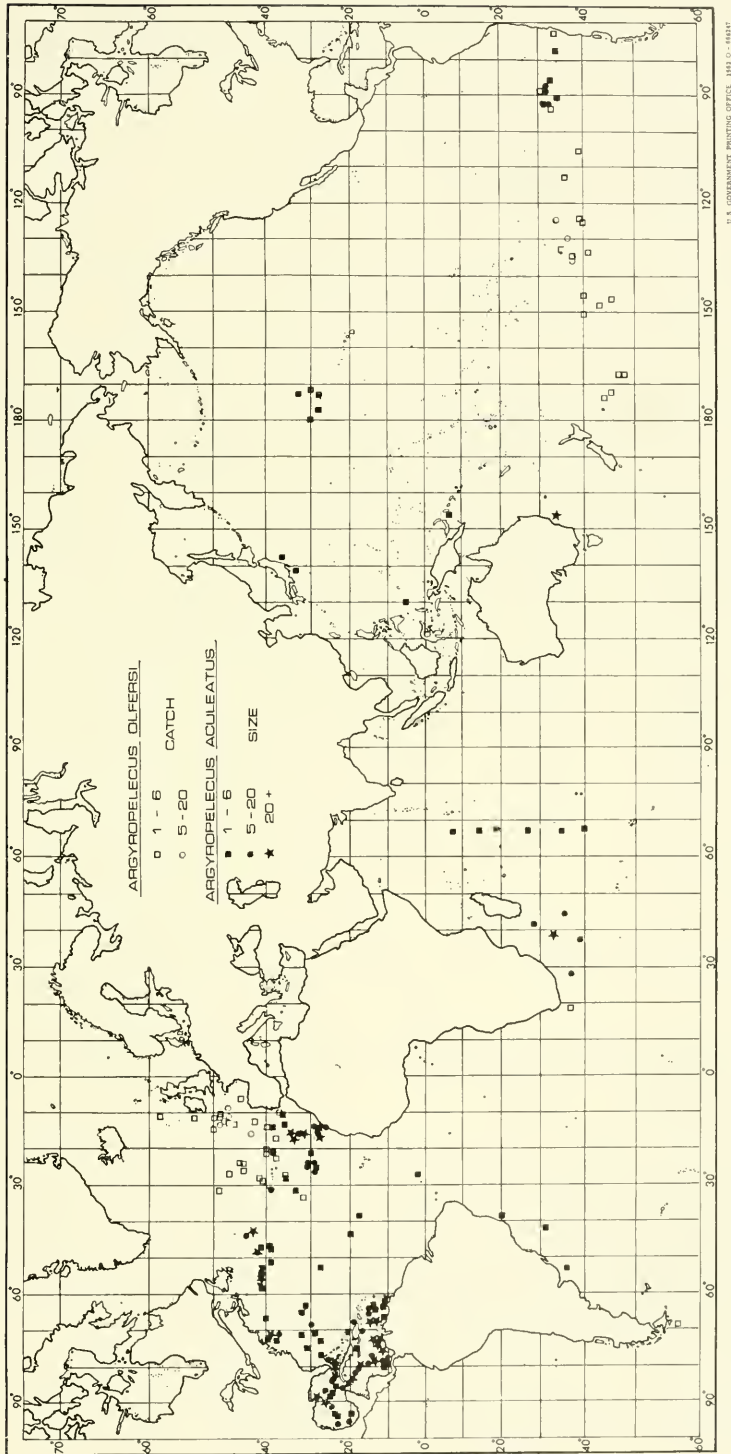


Figure 36. Horizontal distribution of *A. aculeatus* and *A. offersi*. Catch size categories refer to the number of individuals taken in that haul.

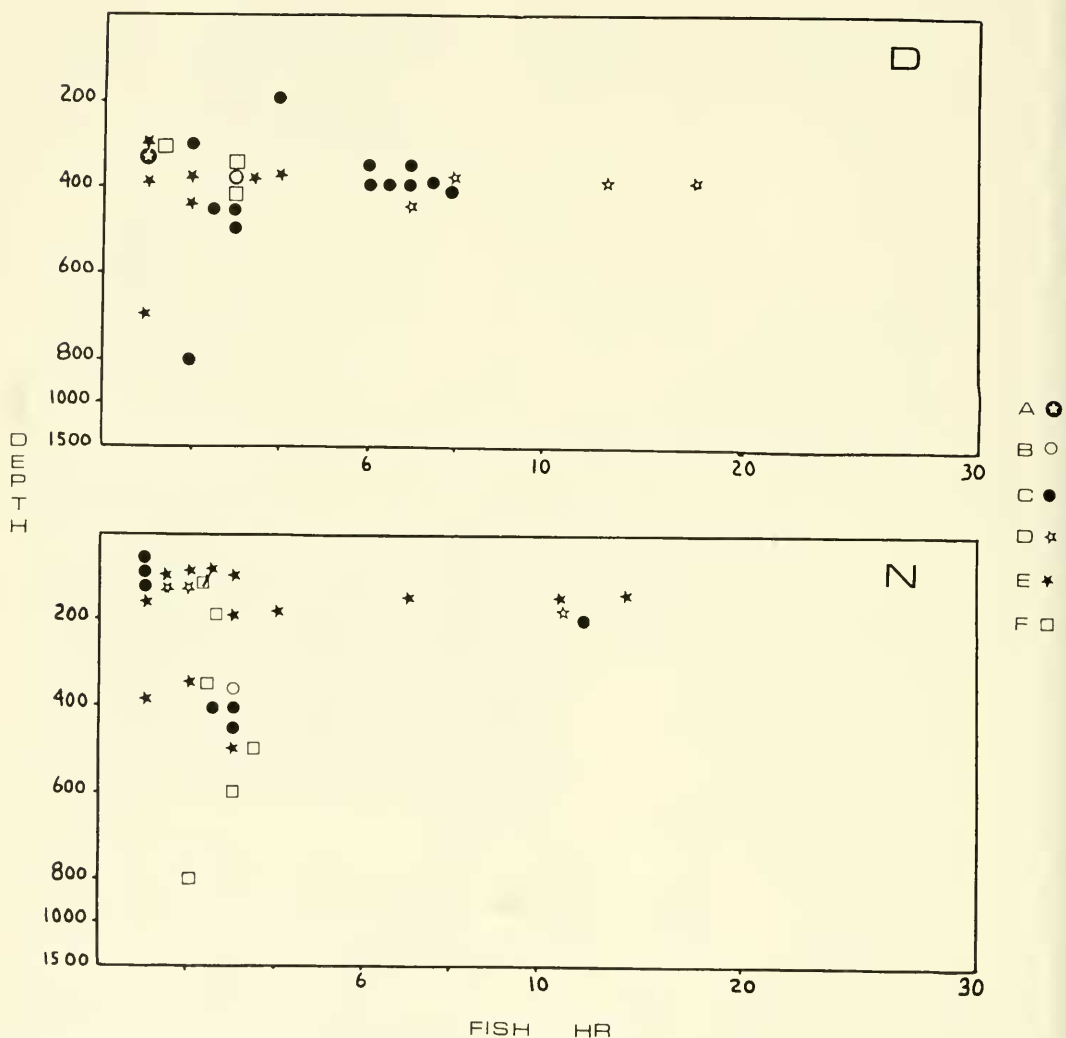


Figure 37. Diurnal vertical distribution of *A. aculeatus* determined by rate of capture with depth during day (D) and night (N). A = Pacific (Chile); B = N Central Pacific; C = Caribbean and Tropical Atlantic; D = NW Atlantic; E = Gulf of Mexico; F = NE Atlantic.

Holt and Byrne, 1913: 120; Jespersen, 1915: 23; 1934: 15; Roule and Angel, 1933: 46; Buen, 1935: 52; Parr, 1937: 49 (spines); Bertin, 1940: 314 (holotype); Nybelin, 1948: 23; Bertelsen and Grontved, 1949: 163 (light organs); Maul, 1949b: 13; Dollfus, 1955: 1; Holgersen, 1958: 120 (population density); Koefoed, 1961: 10; Schultz, 1961: 610; 1964: 241; Wheeler, 1969: 136.

Species distinction. Differs from *A. aculeatus* by absence of subcaudal spines,

less deep body (see regressions, body depth, Tables 8 and 10), lower dorsal spine, higher vertebral count and post-abdominal spine characteristics; differs from *A. lychnus* by presence of enlarged canines, lighter pigment, no subcaudal spines, preopercle and post-temporal spine characteristics and first anal photophore; differs from *A. sladeni* by presence of enlarged canines; no definite pigmented

TABLE 8. REGRESSION STATISTICS FOR VARIOUS POPULATIONS OF *A. ACULEATUS*.

Character	Regression	
	A	B
<i>SE Pacific</i> (Chile)		
Body depth	-1.64	$0.77 \pm .274$
Jaw length	1.27	$0.22 \pm .087$ N = 8
<i>Gulf of Mexico</i> (24°N, 83°W)		
Body depth	0.49	$0.67 \pm .084$
Caudal peduncle depth	0.12	$0.12 \pm .015$
Jaw length	0.70	$0.23 \pm .032$ N = 23
<i>Caribbean</i> (13°N, 71°W) (Sample 1)		
Body depth	2.32	$0.64 \pm .064$
Caudal peduncle depth	0.20	$0.12 \pm .013$
Jaw length	0.70	$0.24 \pm .025$ N = 23
<i>Caribbean</i> (13°N, 71°W) (Sample 2)		
Body depth	2.85	$0.63 \pm .080$
Caudal peduncle depth	0.39	$0.11 \pm .018$
Jaw length	0.66	$0.25 \pm .034$ N = 26
<i>NW Atlantic</i> (42°N, 47°W) (9/64)		
Body depth	0.69	$0.66 \pm .087$
Caudal peduncle depth	-0.06	$0.12 \pm .020$
Jaw length	-0.05	$0.26 \pm .031$ N = 28
<i>NW Atlantic</i> (41°N, 62°W) (9/64)		
Body depth	0.60	$0.67 \pm .061$
Caudal peduncle depth	0.23	$0.12 \pm .012$
Jaw length	-0.17	$0.26 \pm .025$ N = 30
<i>NW Atlantic</i> (42°N, 62°W) (9/62)		
Body depth	0.25	$0.67 \pm .055$
Caudal peduncle depth	0.57	$0.11 \pm .010$
Jaw length	-0.47	$0.27 \pm .038$ N = 40
<i>NE Atlantic</i> (32°N, 13°W)		
Body depth	1.32	$0.69 \pm .123$
Caudal peduncle depth	1.34	$0.10 \pm .019$
Jaw length	-0.72	$0.29 \pm .042$ N = 29

TABLE 9. SLOPE COMPARISONS OF REGRESSIONS OF VARIOUS CHARACTERS BETWEEN TWO POPULATIONS OF *A. ACULEATUS*. THE CARIBBEAN POPULATION CONSISTS OF TWO SUBSAMPLES (SEE TABLE 8).

Character	Population 1	Population 2	T	P
Caudal peduncle depth	NE Atlantic	Caribbean 2	2.009	.05
Jaw length	NE Atlantic	Caribbean 1	2.266	.038
Jaw length	NE Atlantic	Caribbean 2	2.059	.048

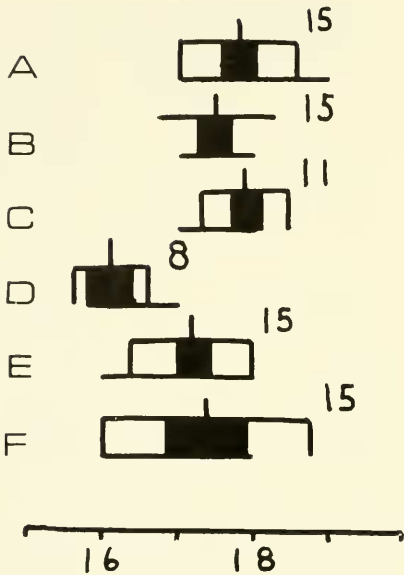


Figure 38. Geographic variation in gill raker count in *A. aculeatus*. A = NW Atlantic; B = NE Atlantic; C = N Central Pacific; D = Pacific (Chile); E = Caribbean; F = Gulf of Mexico. Numbers refer to sample size.

midline; deeper body (see regression, body depth, Table 11), spine characteristics, anal photophores, and lower gill raker count.

Description. D. 9; A. 12; P. 10–11; total gill rakers (15) 16–17; vertebrae 36–37 (38).

Large species often exceeding 70 mm SL; body deep, depth at end of dorsal usually greater than 1.5 times into SL; first preanal photophore with pointed dorsal margin; dorsal spine high, its height nearly one-half its length; post-temporal spines well developed; postabdominal spines nearly equal, anteriormost spine curves smoothly forward; lower preopercle spine long, curving forward, upper very short; jaws large; teeth recurved with two large canines in lower jaw and a somewhat smaller pair in the upper jaw; pigment diffuse over whole of trunk; no marked midline pigment spots; less marked concentration of pigment in caudal peduncle; dark pigment present on outermost caudal rays (this often lost in handling).

TABLE 10. REGRESSION STATISTICS FOR TWO POPULATIONS OF *A. OLFERSI*.

Character	Regression	
	A	B
<i>NE Atlantic</i>		
Body depth	0.51	0.64 ± .231
Jaw length	0.56	0.26 ± .099
		N = 8
<i>Southern Ocean (Pacific)</i>		
Body depth	1.74	0.61 ± .158
Jaw length	-0.19	0.28 ± .075
		N = 10

Distribution. Horizontal distribution (Fig. 36): Restricted to the northeast Atlantic between latitudes 35°N and 65°N and east of longitude 35°W; occurs in a broad band across the southern Pacific between 30°S and 50°S from Chile to New Zealand; reported southwest of the Cape of Good Hope suggesting a bipolar distribution in the Atlantic; not reported from the North Pacific or southern Indian Ocean.

Vertical distribution (Fig. 41): Data variable by day with relatively low concentrations from 200 m to 750 m; by night depths are concentrated between 200 m and 450 m with most records from 180 m to 300 m; no indications of marked geographic variation in depth.

Geographic variation. Analysis of small sample sizes from the two major widely separated populations indicate no statistical differences and little evidence of separation (Table 10; Fig. 42).

Argyrolepiscus sladeni Regan
Figure 43

Argyrolepiscus sladeni Regan, 1908: 218 (holotype BMNH; Central Indian Ocean; not seen); Jespersen, 1934: 15; Fowler, 1936: 1208; Parr, 1937: 49 (fig., incorrectly cites Norman, 1930 as original description); Norman, 1939: 19;

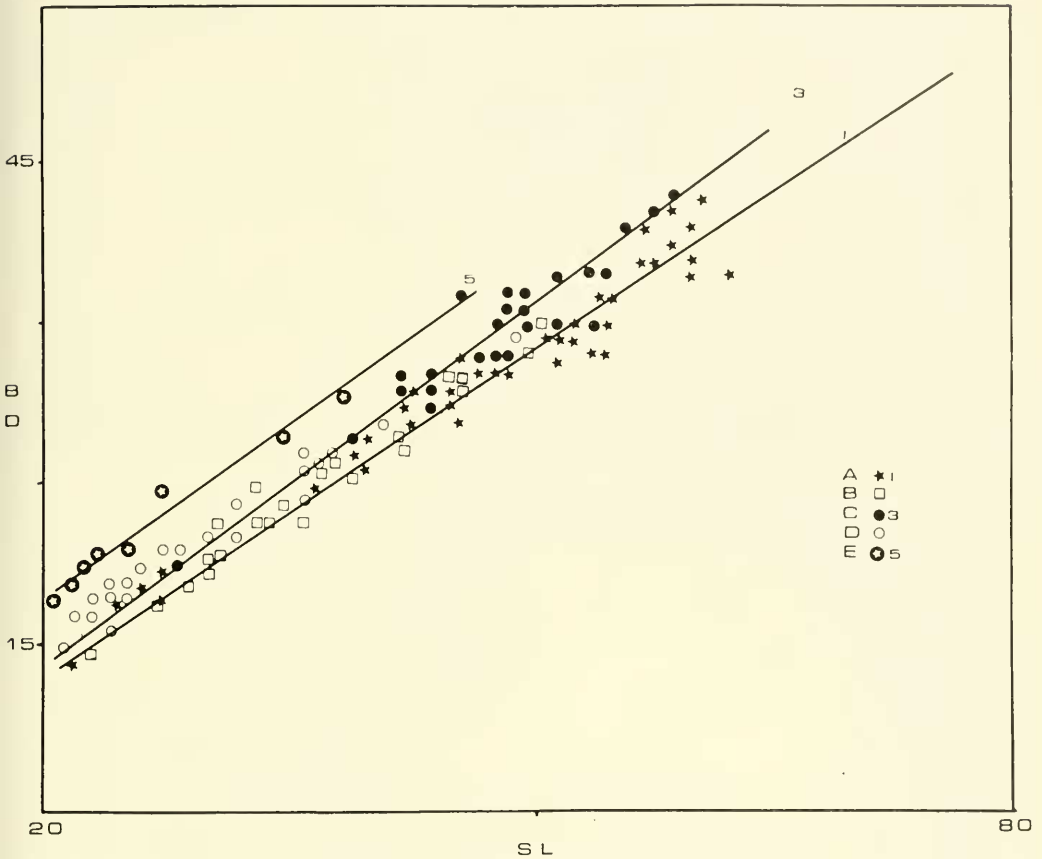


Figure 39. Geographic variation in the regression of body depth (BD) on standard length (SL) in *A. aculeatus*. A = NW Atlantic; B = Gulf of Mexico; C = NE Atlantic; D = Caribbean; E = Pacific (Chile).

Marr, 1948: 140; Misra, 1952: 367; Haig, 1955: 321; Fowler, 1956: 27; Koefoed, 1961: 1.

Argyrolepecus olfersi: Barnard, 1925: 153; Smith, 1957: 37 (?); Bright and Paquegnat, 1969: 29. *Argyrolepecus lychnus lychnus* Schultz, 1961: 587 (in part); 1964: 241; Blache, 1964: 71; Backus et al., 1965: 139; Bright and Paquegnat, 1969: 30.

Argyrolepecus lychnus sladeni Schultz, 1961: 587; 1964: 241 (incorrectly cites Norman, 1930. as original description); Kotthaus, 1967: 22 (photo., otoliths).

Argyrolepecus lychnus hawaiiensis Schultz, 1961: 587; 1964: 241.

Argyrolepecus hawaiiensis Berry and Perkins, 1965: 625; Lavenberg and Ebeling, 1967: 185.

Species distinction. See *A. olfersi* (p. 52) and *A. lychnus* (p. 63).

Description. D. 9; A. 12; P. 10–11; total gill rakers 17–21; vertebrae 35–37.

Medium size species seldom exceeding 60 mm SL; body less deep, depth at end of dorsal about two or more times into SL; dorsal blade low, height about three or more times into its length; postabdominal spines of equal size, anterior one occasionally straight, usually squared or blunted; upper preopercle spine long, directed posteriorly and usually dorsally, lower directed ventrally and often slightly posteriorly; jaws medium; teeth small, recurved, no large canines present; gill rakers medium to long, slightly dentate; first pre-anal photophore raised well above second

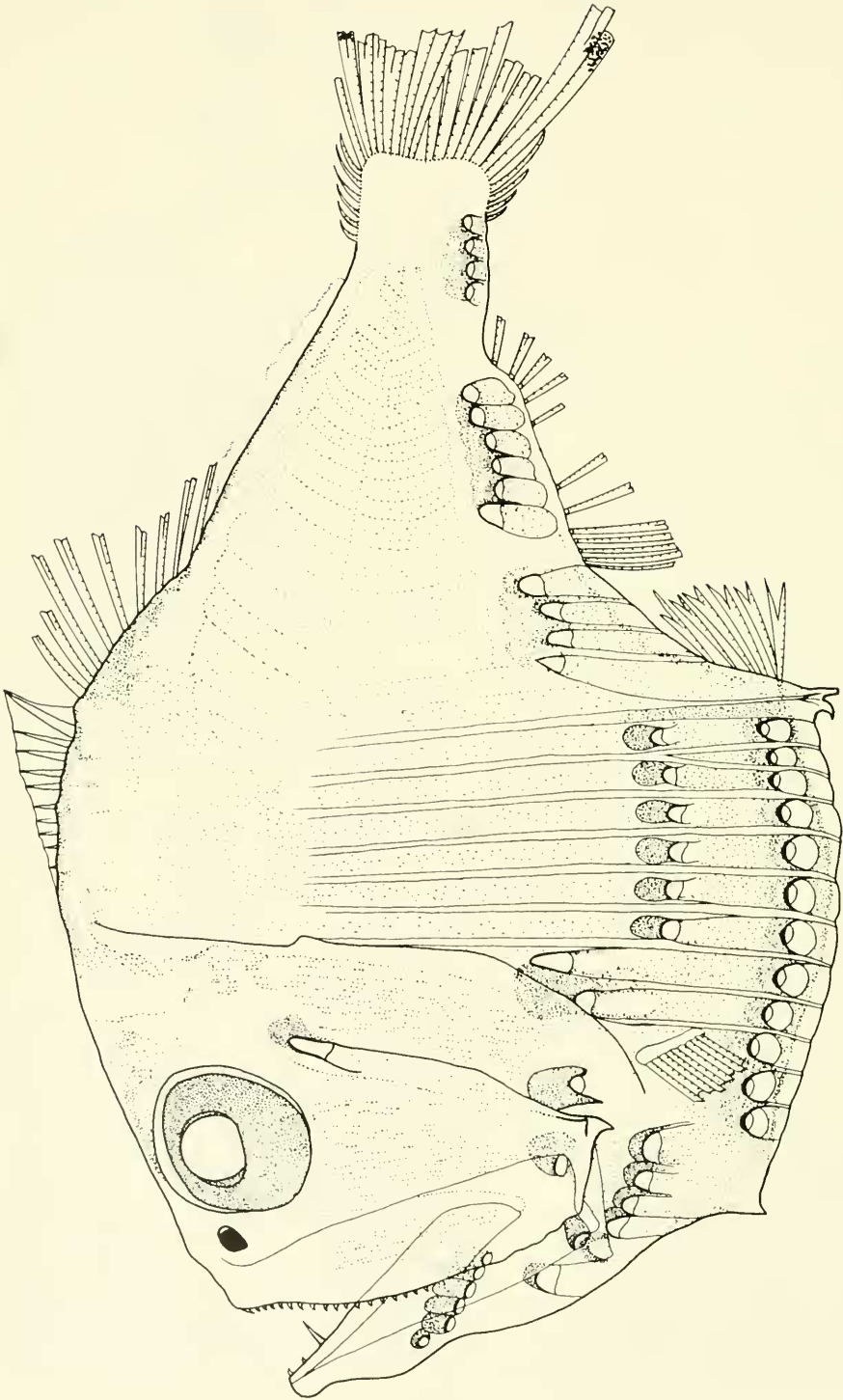


Figure 40. *Argyropelecus olfersi*; R/V ATLANTIS II, Cruise 13; Station 1039; SL 50 mm.

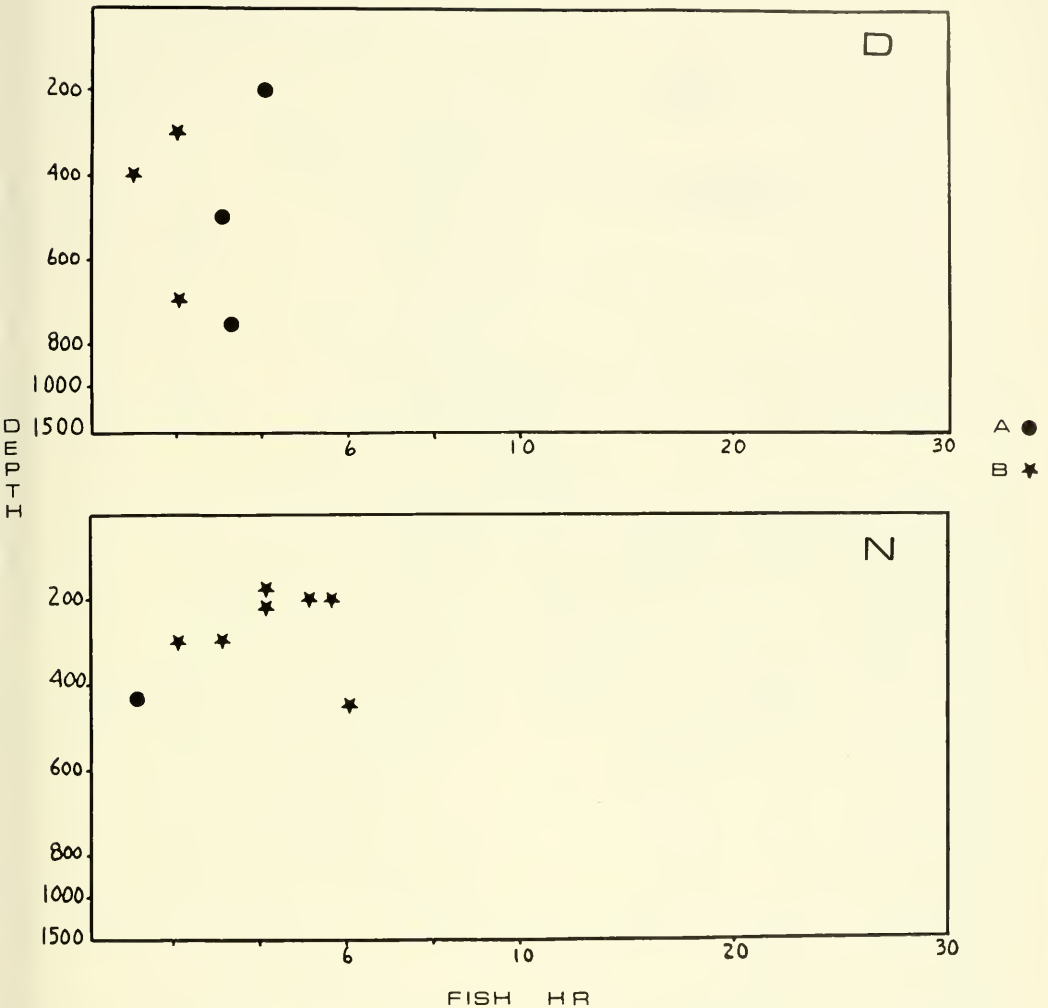


Figure 41. Diurnal vertical distribution of *A. offersi* determined by rate of capture with depth. A = Southern Ocean (Pacific); B = NE Atlantic.

which is even with or above third; anal pterygiophore gap with three haemal spines lacking pterygiophores; in preservative pigment often quite dark; large distinct pigment spots present along midline, especially evident in smaller specimens; there may be a diurnal pigment difference similar to *A. hemigymnus* in this species.

Distribution. Horizontal distribution (Fig. 44): In the Atlantic this species is found in abundance along the African coast from

about 15°S northward into the Gulf of Guinea; it occurs in moderate numbers across the equatorial Atlantic in a belt from 5°S to 15°N latitude; it is abundant in the Caribbean in the vicinity of the Venezuelan coast, absent from the northern Caribbean, appearing again in numbers in the western and northern Gulf of Mexico and the straits of Florida; a few small catches have been taken in the North Atlantic and along the Brazilian coast. In

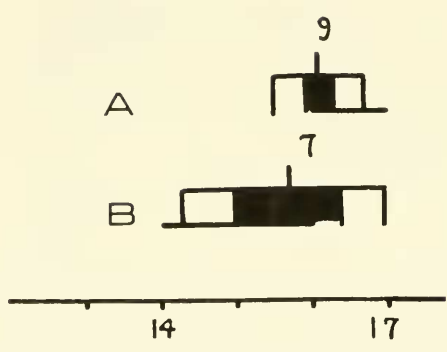


Figure 42. Geographic variation in gill raker count in *A. olfersi*. A = NE Atlantic; B = Southern Ocean. Numbers refer to sample size.

the Pacific a somewhat biantitropical distribution is indicated, with large populations represented in the North Pacific to about 175°W longitude, and off the California coast; another large population occurs off the coast of Chile; the species occurs north of New Zealand and south of Hawaii. *A. sladeni* is abundant in the northern Indian Ocean to about 15°N and along the African coast to about 10°S; while not reported from the Bay of Bengal, it is represented by several small catches south of Java.

Vertical distribution (Fig. 45): Concentrated between 350 m and 600 m by day, with the major concentrations between 350 m and 450 m; by night concentrated between 100 m and 375 m, with the major concentrations between 100 m and 300 m; no marked indication of geographic variation with depth.

Geographic variation. This species, like *A. gigas*, has low variability in those body

TABLE 11. REGRESSION STATISTICS FOR VARIOUS POPULATIONS OF *A. SLADENI*.

Character	Regression	
	A	B
<i>N Pacific</i> (42°N, 165°W)		
Body depth	0.38	0.52 ± .156
Dorsal blade	2.02	0.01 ± .027
Jaw length	-0.03	0.25 ± .076
Jaw width	0.48	0.13 ± .070
		N = 10
<i>E Pacific</i> (California)		
Body depth	1.25	0.53 ± .074
Dorsal blade	2.62	0.00 ± .022
Jaw length	0.92	0.23 ± .027
Jaw width	0.62	0.10 ± .028
		N = 27
<i>Indian Ocean</i> (05°N, 65°E)		
Body depth	0.80	0.56 ± .142
Dorsal blade	1.89	0.01 ± .010
Jaw length	0.22	0.24 ± .069
Jaw width	-0.73	0.13 ± .043
		N = 11
<i>Caribbean</i>		
Body depth	0.87	0.52 ± .163
Dorsal blade	1.29	0.02 ± .013
Jaw length	-0.07	0.26 ± .081
Jaw width	0.75	0.12 ± .044
		N = 9
<i>Gulf of Guinea</i>		
Body depth	-0.91	0.57 ± .110
Dorsal blade	1.89	0.01 ± .014
Jaw length	-0.33	0.27 ± .055
Jaw width	1.14	0.11 ± .027
		N = 13
<i>SE Pacific</i> (Chile)		
Body depth	0.51	0.54 ± .097
Dorsal blade	2.04	0.01 ± .012
Jaw length	1.04	0.23 ± .040
Jaw width	-0.63	0.14 ± .035
		N = 16

TABLE 12. COMPARISONS BETWEEN MEAN SLOPES OF TWO CHARACTERS FOR ALL POPULATIONS OF *A. SLADENI* AND *A. LYCHNUS* FOR WHICH REGRESSION STATISTICS WERE CALCULATED. POP. # = NUMBER OF POPULATIONS; \bar{x} SLOPE = UNWEIGHTED MEAN SLOPE; TOTAL # = TOTAL NUMBER OF FISH MEASURED OVER ALL POPULATIONS.

Species	Character	Pop. #	\bar{x} Slope	Range	Total #
<i>A. sladeni</i>	body depth	6	0.54	0.52-0.57	86
<i>A. lychnus</i>	body depth	3	0.61	0.57-0.64	38
<i>A. sladeni</i>	jaw width	6	0.12	0.10-0.14	86
<i>A. lychnus</i>	jaw width	3	0.15	0.14-0.16	38

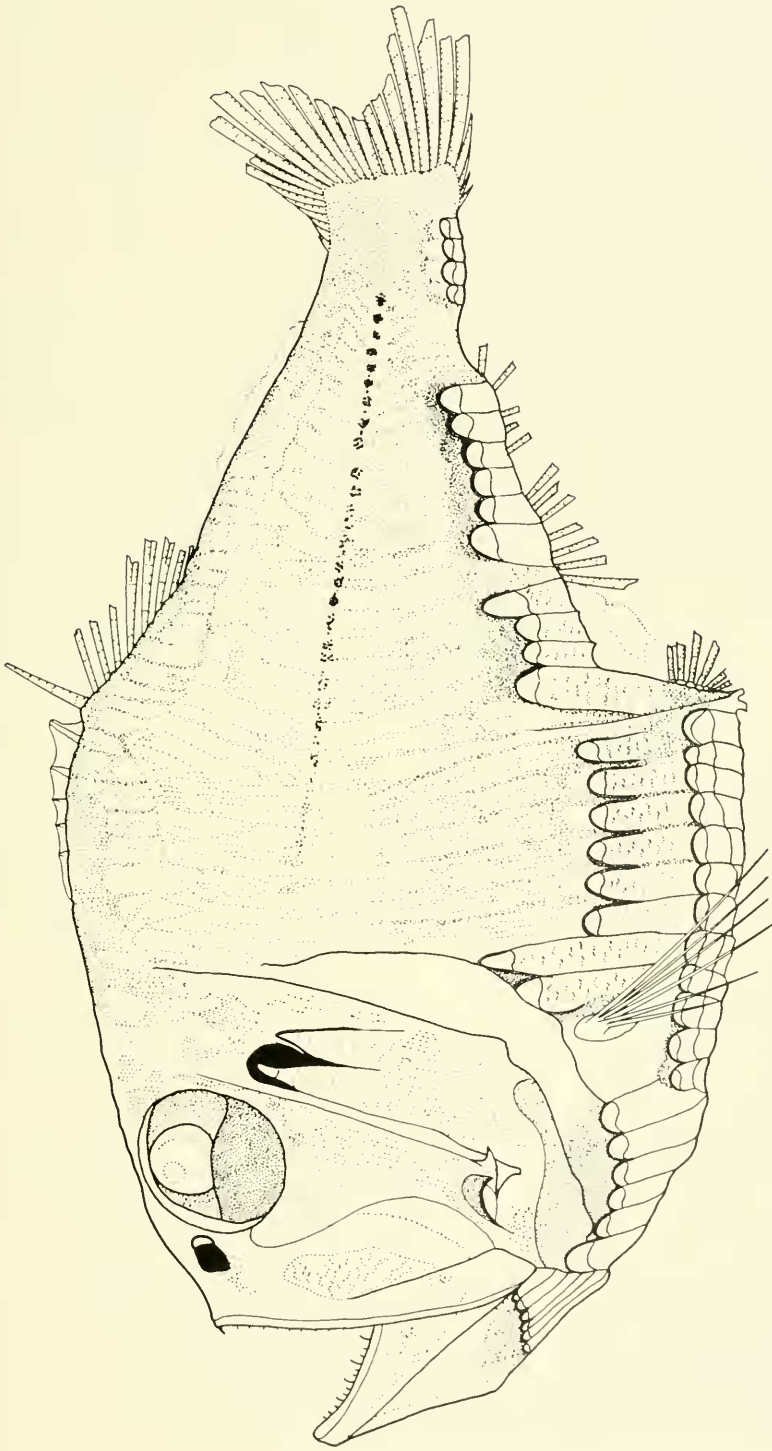


Figure 43. *Argyropelecus sladeni*; R/V CHAIN, Cruise 60; Station 1296; SL 43 mm.

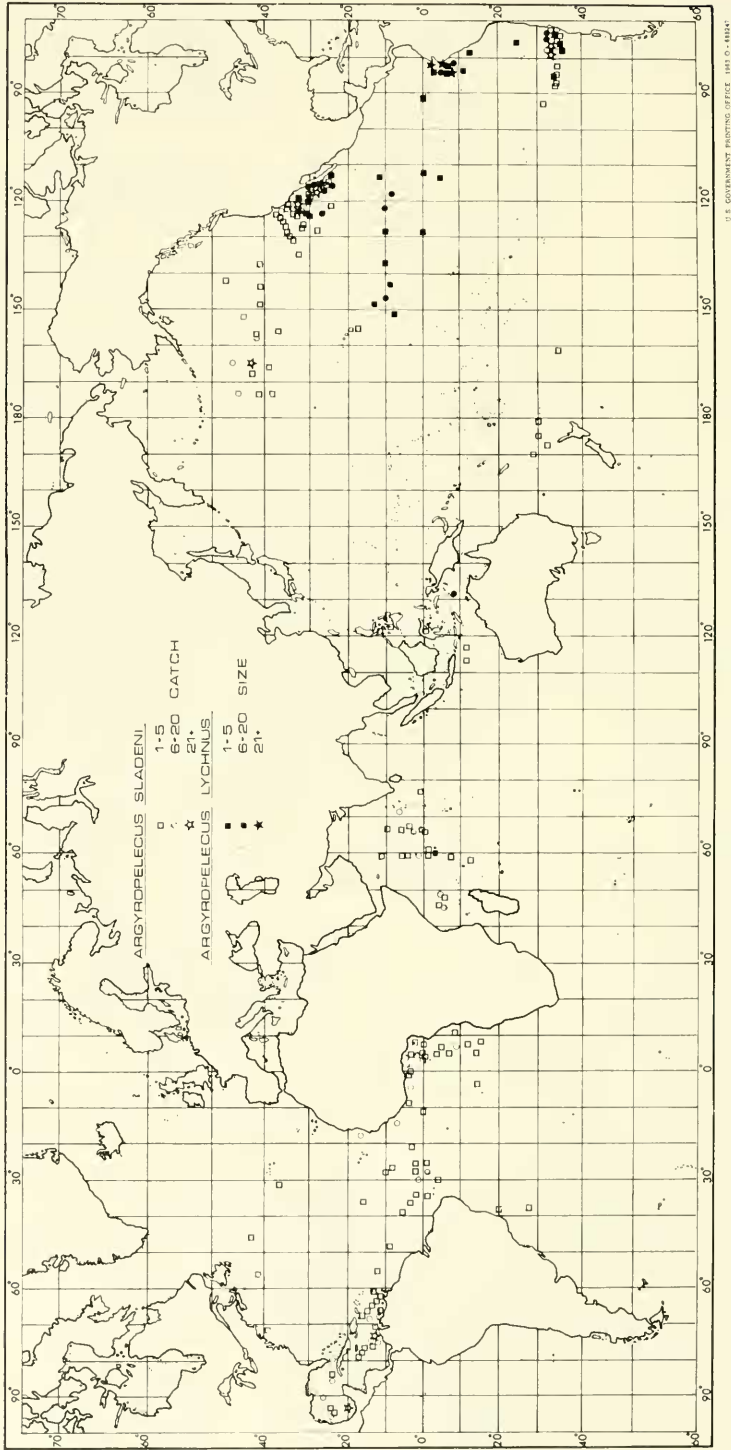


Figure 44. Horizontal distribution of *A. sladeni* and *A. lychnus*. Catch size categories refer to the number of individuals taken in that haul.

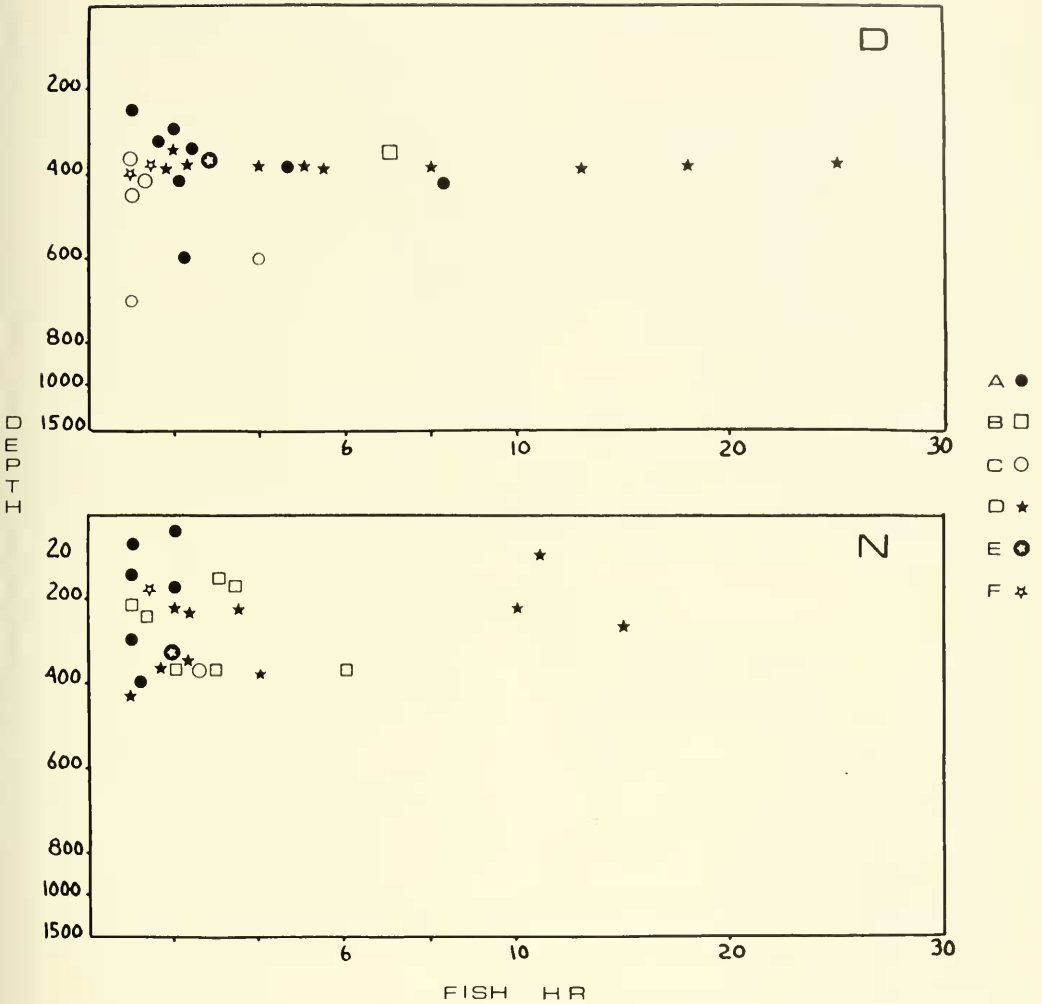


Figure 45. Diurnal vertical distribution of *A. sladeni* determined by rate of capture with depth during day (D) and night (N). A = Pacific (California); B = Pacific (Chile); C = Gulf of Guinea; D = Gulf of Mexico and Caribbean; E = N Central Pacific; F = N Atlantic.

proportions measured. Overlap is broad and sample sizes are small. Six populations were statistically defined (Table 11; Fig. 46) but only gill raker counts gave much separation. Certainly the Atlantic population is distinct from the Indian Ocean and several Pacific populations; within the latter, distinctions are not marked. The Indian Ocean, Chile, and California populations show some separation, although not statistically significant. Other characters

and larger sample sizes are required to better define populations in this species.

Argyrolepecus lychnus Garman Figure 47

Argyrolepecus lychnus Garman, 1899: 234 (lectotype USNM 57885, designation Schultz, 1961; tropical east Pacific, not seen; paralectotype MCZ 35193, seen); Ledenfeld, 1905: 170 (light organs); Berry and Perkins, 1965: 625; Grandperrin and Rivaton, 1966: 36; Lavenberg and Ebeling, 1967: 185.

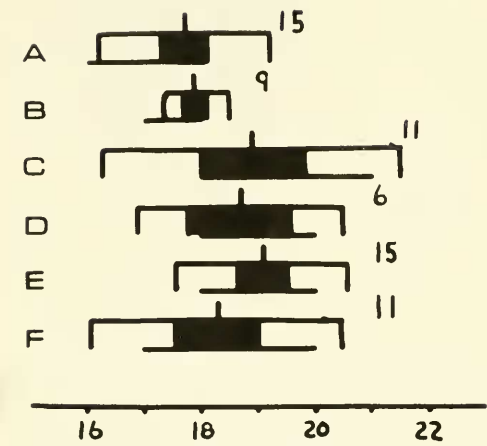


Figure 46. Geographic variation in gill raker count in *A. sladeni*. A = Gulf of Guinea; B = Caribbean; C = Indian Ocean; D = N Central Pacific; E = Pacific (Chile); F = Pacific (California). Numbers refer to sample size.

Argyrolepecus olfersi: Weber and DeBeaufort, 1913: 1 (?); Clemens and Wilby, 1949: 106; Koumans, 1953: 186 (?); Morrow, 1957: 56; Koepeke, 1962: 145; Bussing, 1965: 185.
Argyrolepecus lychnus lychnus Schultz, 1961: 587 (in part); 1964: 241.
Argyrolepecus sp., Kotthaus, 1967: 11 (?) (photo.).

Species distinction. See *A. olfersi* (p. 52); differs from *A. sladeni* by its higher dorsal blade, preopercle spine characteristics, presence of two rather than three haemal spines in anal pterygiophore gap,

lack of distinct dark pigment spots on midline, broader body, and generally lower gill raker count (Figs. 46 and 49). Tables 12 and 13 and Figure 50 illustrate the nature and degree of difference in several of the characters mentioned above.

Description. D. 9; A. 12; P. 10–11; total gill rakers 16–18; vertebrae 35–37.

Medium to large species often exceeding 60 mm SL; body deep, depth at end of dorsal greater than 1.5 into SL; dorsal blade high, height about 2.5 times into its length; postabdominal spines of about equal size, anterior one slightly smaller, not smoothly curving but blunted or squared; upper preopercle spine long, directed posteriorly and usually ventrally; lower spine usually curved slightly anteriorly or straight down; jaws large, teeth recurved especially in lower jaw, no large canines; gill rakers medium to short, dentate; first preanal photophore usually lower than third; spiny scales present in adults below subcaudal photophores; the gap made by the anal pterygiophores contains two haemal spines lacking pterygiophores; in preservative, pigment dark dorsally, diffuse on trunk with small, light pigment spots on midline.

Distribution. Horizontal distribution (Fig. 44): Absent from the Atlantic; represented possibly by a single sample from the Indian Ocean (04°S, 60°E, Kotthaus, 1967). Pri-

TABLE 13. SLOPE COMPARISONS OF THE REGRESSION OF DORSAL BLADE HEIGHT ON STANDARD LENGTH FOR VARIOUS POPULATIONS OF *A. LYCHNUS* (L) AND *A. SLADENI* (S).

Character	Population 1—L	Population 2—S	T	P
Dorsal blade	C Pacific	Chile	3.179	.005
	C Pacific	N Pacific	2.452	.025
	C Pacific	Indian	2.904	.01
	Chile	Chile	3.903	.001
	California	Chile	3.965	.001
	Chile	N Pacific	2.171	.045
	Chile	California	3.514	.001
	Chile	Indian	3.366	.005
	California	N Pacific	2.272	.035
	California	California	3.355	.005
	California	Indian	3.444	.005

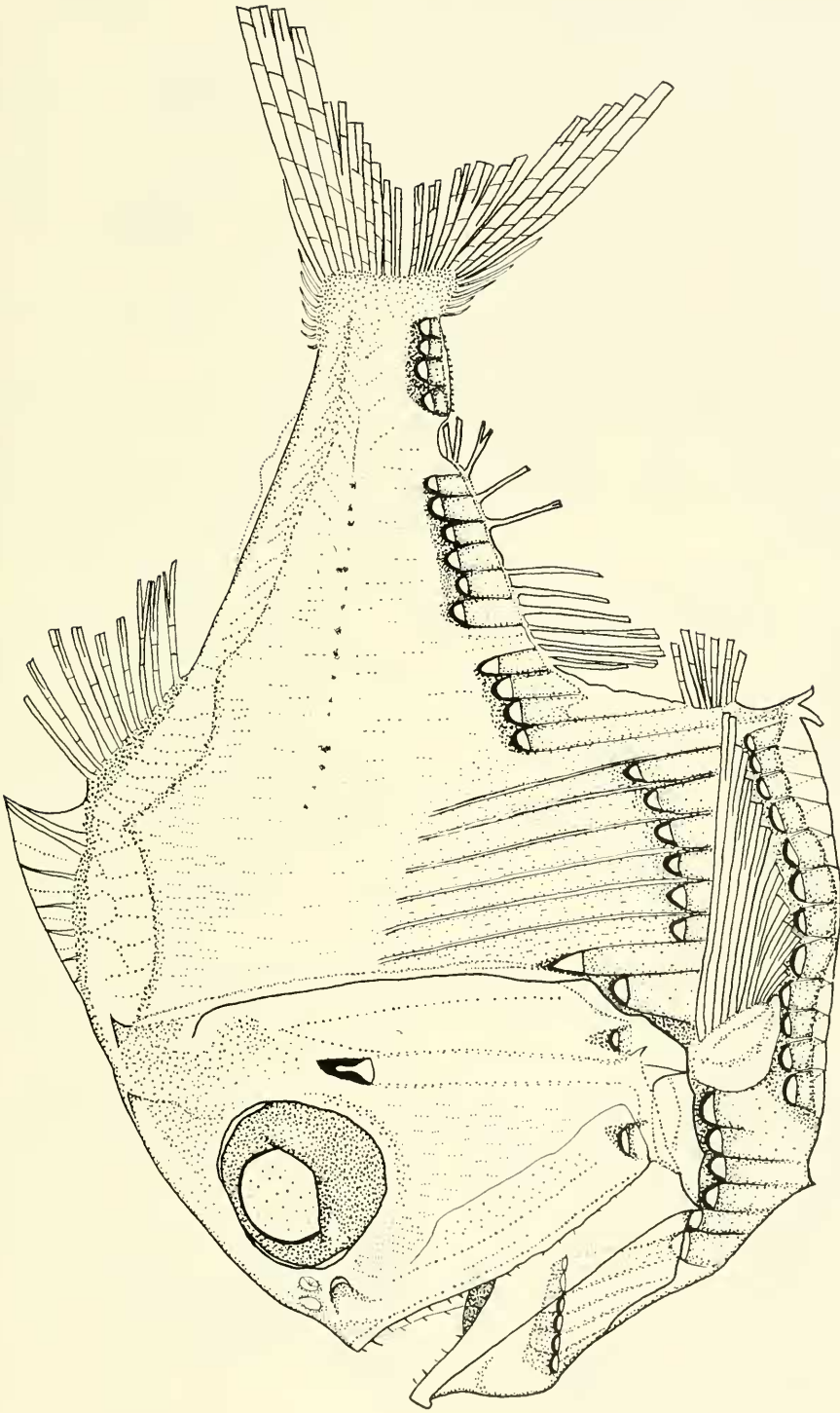


Figure 47. *Argyropelecus lychnus*; R/V HUGH M. SMITH, Cruise 31; Station 50; SL 40 mm.

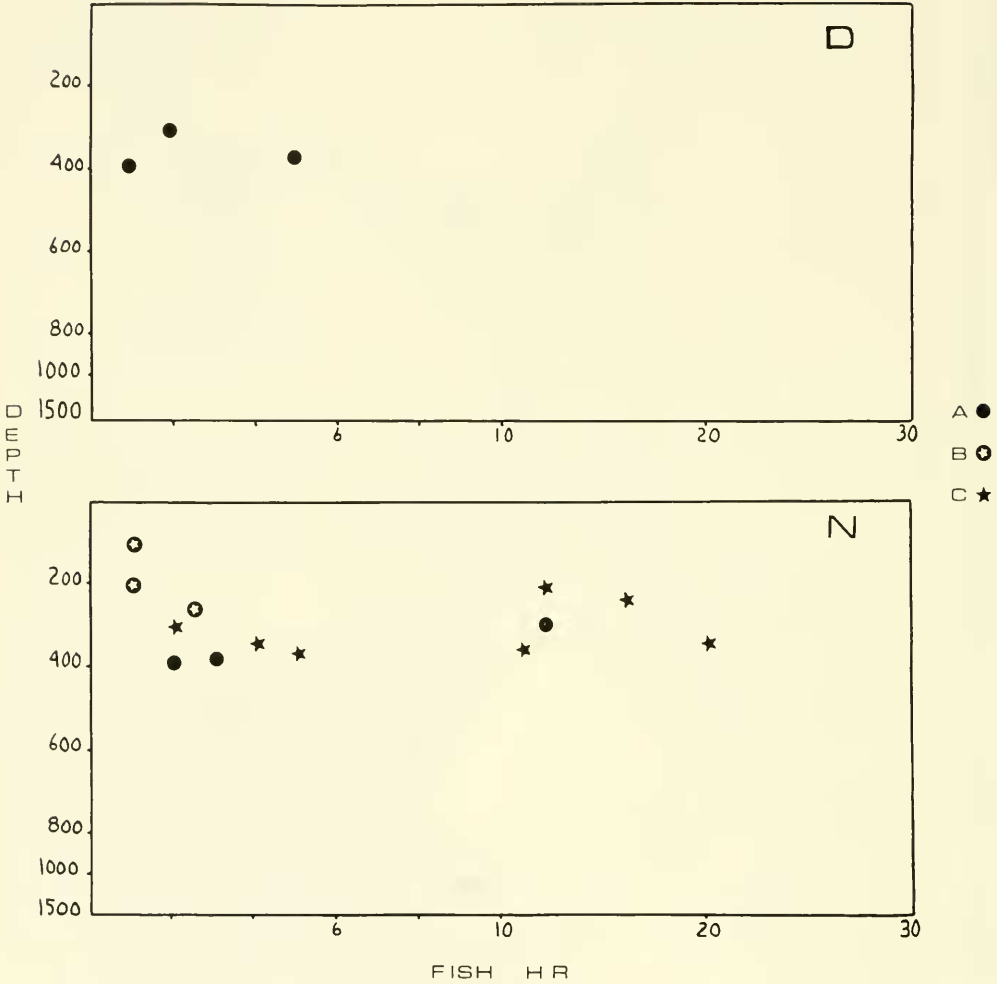


Figure 48. Diurnal vertical distribution of *A. lychnus* determined by rate of capture with depth during the day (D) and night (N). A = Pacific (California); B = Pacific (Chile); C = Tropical E Pacific.

marily restricted to the tropical Pacific; found in abundance in the eastern Pacific between 35°N and 35°S; distribution narrows across the equatorial Pacific as far as 160°W; a moderate catch from the lesser Sunda Islands indicates a possible trans-equatorial distribution in the Pacific.

Vertical distribution (Fig. 48): Concentrated between 300 m and 400 m off California by day, with the highest concentration near 400 m; by night major

concentrations occur from 200 m to 350 m, with no marked indication of geographical variation in depth.

Geographic variation. Three samples from widely separated areas in the tropical east Pacific and its northern and southern boundaries gave no indication of any significant variation (Table 14; Fig. 49). Horizontal distribution data indicates an essentially continuous distribution in this area.

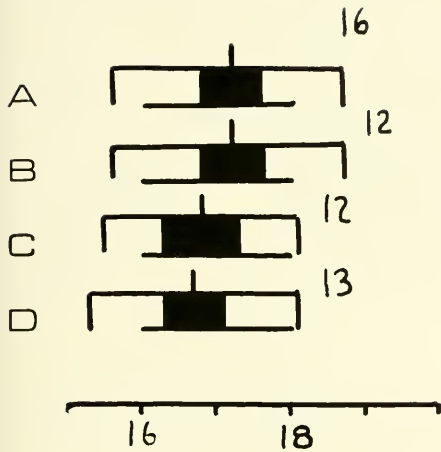


Figure 49. Geographic variation in gill raker count in *A. lychnus*. A = Central Pacific; B = Tropical E Pacific; C = Pacific (Chile); D = Pacific (California). Numbers refer to sample size.

Genus *Sternoptyx* Hermann, 1781

Sternoptyx Hermann, 1781: 8 (type species: *Sternoptyx diaphana* Hermann, 1781, by monotypy).

Diagnosis. Ten abdominal, three anal, three branchiostegal and five isthmus photophores; a single large dorsal pterygiophore spine with an anterior, serrated extension; first anal pterygiophore greatly enlarged, forms support for triangulate membrane above anal fin rays; premaxilla without anterior pedicels; anteriormost gill rakers reduced to toothed ridges; post-temporal and supracleithrum separate; hypural elements fused to form single caudal plate; haemal and neural spines greatly elongate in trunk region.

Description. Photophores: PO 1; PTO 1; PRO 1; SO 1; SP 3; PAN 3; SAN 1; AN 3; SC 4.

Spines: Preopercle with single ventrally oriented spine; retroarticular bears spine, preabdominal spine present; basipterygia fused to form a set of four postabdominal spines; base of first anal pterygiophore bears ventral spines; no well-developed post-temporal spines.

TABLE 14. REGRESSION STATISTICS FOR VARIOUS POPULATIONS OF *A. LYCHNUS*.

Character	Regression	
	A	B
<i>SE Pacific</i> (Chile)		
Body depth	2.38	$0.57 \pm .120$
Dorsal blade	1.56	$0.05 \pm .018$
Jaw length	0.84	$0.26 \pm .055$
Jaw width	-0.46	$0.16 \pm .043$
		N = 12
<i>E Pacific</i> (California)		
Body depth	0.94	$0.61 \pm .107$
Dorsal blade	1.53	$0.04 \pm .013$
Jaw length	-0.15	$0.29 \pm .058$
Jaw width	-1.02	$0.16 \pm .031$
		N = 15
<i>Central Pacific</i> (10°N, 145°W)		
Body depth	1.42	$0.64 \pm .156$
Dorsal blade	1.79	$0.05 \pm .023$
Jaw length	0.88	$0.28 \pm .068$
Jaw width	-0.77	$0.14 \pm .052$
		N = 11

Eyes: Large, well developed, nonteleoscopic.

Gill rakers: Total seven to nine; well developed, with rough spiny margins; anteriormost rakers reduced to spiny tooth-like plates extending into mouth cavity.

Jaws and dentition: Jaws vertically oriented, premaxilla small, heavily toothed; maxilla heavily toothed and major upper jaw bone in gape; lower jaw heavily toothed, teeth small, sharp, triangulate; palatine teeth present; first epibranchial extended anteriorly and ventrally forming toothed arms at dorsal, posterior end of mouth.

Meristics: Vertebrae 28-31; C. 9+10; D. 8-11; A. 14-16.

Color: Bright silvery in life, dark pigment especially evident on dorsal surface;

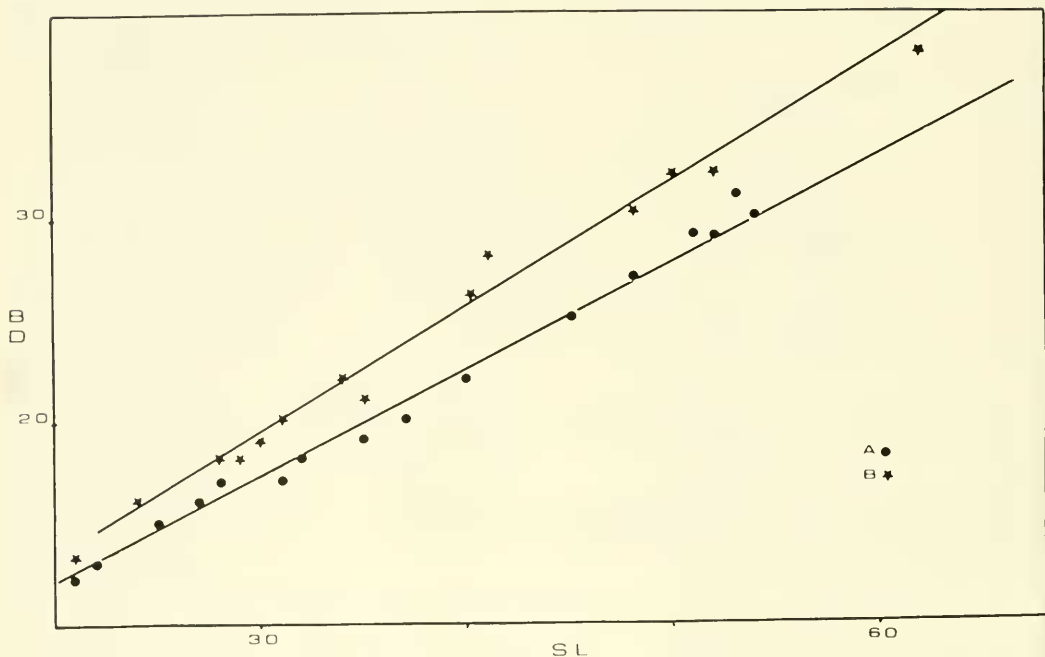


Figure 50. Regression of body depth (BD) on standard length (SL) in *A. sladeni* (A) and *A. lychnus* (B) off California.

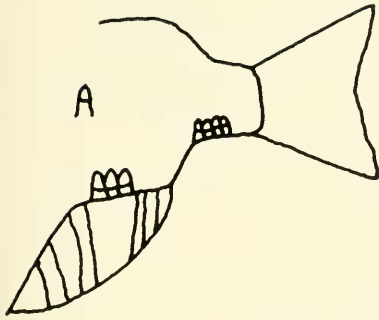
silver quickly lost in formalin preservative; sides can be very dark, often black.

Internal anatomy: Air bladder and gas gland well developed and fills much of the body cavity (see Marshall, 1960); digestive system simple, consisting of a heavily pigmented, single sectioned stomach, capable of considerable distension,

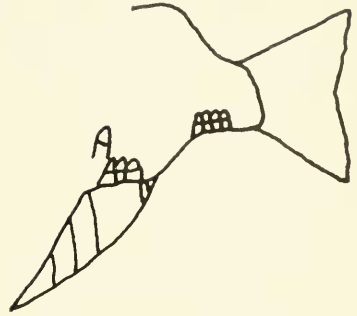
five to seven pyloric caecae of which only two to three are long and well developed, relatively small liver and short, uncoiled, thin-walled intestine. The gonads, when mature, lie against the posterior wall of the body cavity. This cavity is large, unlined with pigment, and appears capable of some expansion.

KEY TO THE SPECIES OF *Sternoptyx*

- 1a. Dorsal long, its length greater than 1.3 times height of dorsal spine; trunk long and narrow, SL more than 3.0 times body depth at end of dorsal (see regression, body depth, Table 15); body very dark, pigment forms broad band at base of caudal rays *S. obscura* (p. 69).
- b. Dorsal short, its length less or equal to height of dorsal spine; trunk broad, SL less than 2.8 times body depth at end of dorsal (see regression, body depth, Tables 16 and 17); body pigment less uniformly dark, pigment absent or in very narrow band at base of caudal rays 2
- 2a. Supra-anal photophore high, its height greater than one-half the distance from ventral body margin to midline (often raised to midline); gill raker tooth plates with prominent spines; secondary anal pterygiophores long, extending posteriorly on same level as anal photophores *S. pseudobscura* (p. 72).
- b. Supra-anal photophore low, its height less than one-half distance from ventral body margin to midline; gill raker tooth plates lacking prominent spines; secondary anal pterygiophores short; not extending posteriorly on same level as anal photophores *S. diaphana* (p. 75).



a.



b.

Sternoptyx obscura Garman
Figure 51

Sternoptyx obscura Garman, 1899: 63 (lectotype USNM 177888; designation Schultz, 1961; tropical east Pacific; not seen; paralectotype MCZ 28532; seen); Ledenfeld, 1905: 170 (light organs); Follett, 1952: 409.

Sternoptyx diaphana Schultz, 1961: 587 (in part); 1964: 241 (in part); Berry and Perkins, 1965: 625 (in part).

Species distinction. Differs from both *S. diaphana* and *S. pseudobscura* in its shorter dorsal spine and longer dorsal fin; longer, narrower trunk, slight extension of body

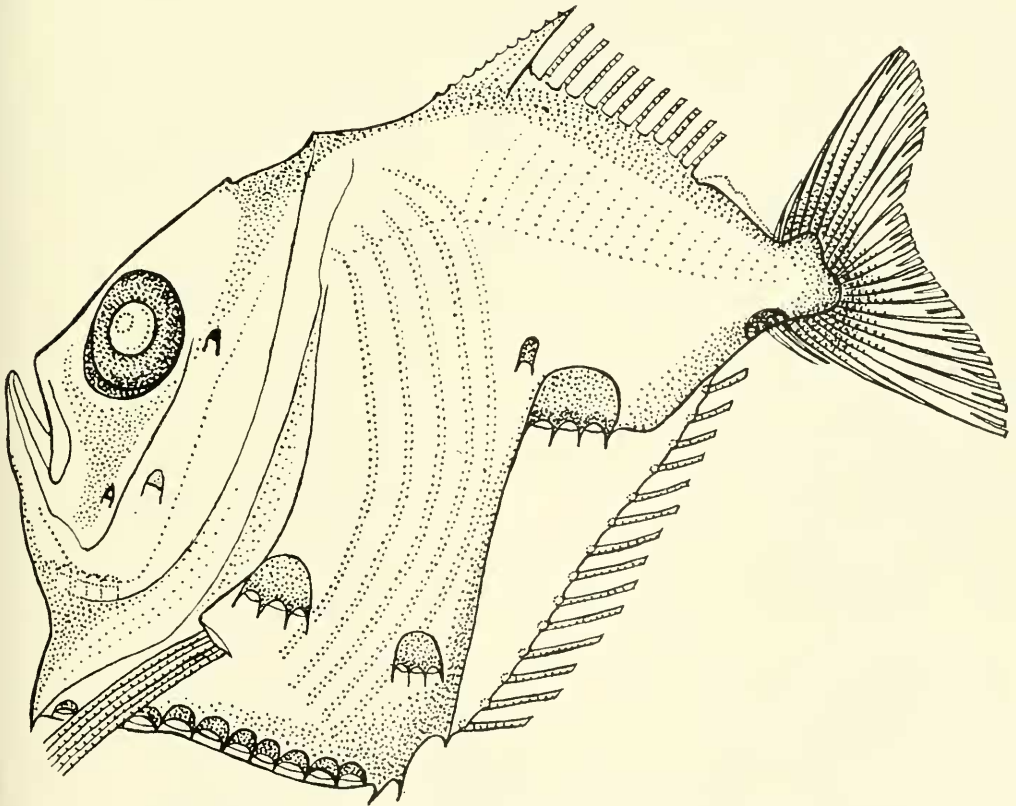


Figure 51. *Sternoptyx obscura*; R/V ANTON BRUUN, Cruise 3; Station 215; SL 30 mm.

margin in front of anal photophores, broad pigment band on base of caudal rays, and generally dark pigment; differs from *S. pseudobscura* in its lower supra-anal photophore, small teeth, low gill raker tooth plates, and smaller mouth; from *S. diaphana* in its extension of the ventral body margin at same level behind anal photophores. Tables 18 and 19, and Figures 53, 56, and 61 illustrate the degree of difference between the three species in several of the above characters. Note especially the significant differences between sympatric populations.

Description. D. 10–11; A. 14–15; P. 10–11; total gill rakers 7–9; vertebrae 29 (30).

Small species, seldom exceeds 40 mm SL; trunk long and narrow, its length usually longer than depth; dorsal fin long, its length more than 1.3 times the length of dorsal spine; abdominal length along midline from supra-anal photophore to caudal peduncle, less than or equal to body depth at end of dorsal; postabdominal and anal pterygiophore spines long; posterior anal pterygiophores extend behind and at same level with anal photophore group; supra-anal photophore raised above anals one half or less the distance to midline; body margin extends slightly in front of anal photophores before curving ventrally; jaws medium; teeth small; gill raker tooth plates consist of multiple low spiny ridges; anterior dorsal surface of tongue between branchial arches smooth; few-to-no raised nodules; in preservative, pigment very dark over whole of body; pigment extends in broad band at base of caudal fin rays.

Distribution. Horizontal distribution (Fig. 52): This species has not been recorded from the Atlantic; it is concentrated north of 10°S latitude in the Indian Ocean, although small catches occur as far as 40°S; occurs in the eastern Bay of Bengal, and abundantly south of Java; occurs off the Philippines and scattered but large catches indicate in all probability a continuous distribution across the equatorial Pacific; occurs abundantly in the tropical east

TABLE 15. REGRESSION STATISTICS FOR VARIOUS POPULATIONS OF *S. OBSCURA*.

Character	Regression	
	A	B
<i>Indian Ocean</i> (5°N, 60°E)		
Body depth	-0.35	0.31 ± .051
Abdominal length	-1.16	0.40 ± .074
		N = 23
<i>Indian Ocean</i> (3°N, 67°E)		
Body depth	0.45	0.29 ± .133
Jaw length	2.41	0.09 ± .067
		N = 10
<i>Java</i> (10°S, 114°E)		
Body depth	0.98	0.27 ± .071
Abdominal length	0.68	0.31 ± .090
		N = 25
<i>Central Pacific</i> (11°N, 163°E)		
Body length	-1.72	0.37 ± .067
Abdominal length	0.12	0.37 ± .074
Jaw length	0.85	0.14 ± .028
		N = 20
<i>Central Pacific</i> (7°S, 135°W)		
Body depth	-0.71	0.34 ± .104
Abdominal length	0.71	0.35 ± .141
Jaw length	0.10	0.15 ± .057
		N = 11
<i>East Pacific</i> (California)		
Body depth	-0.94	0.33 ± .075
Abdominal length	-1.23	0.42 ± .091
Jaw length	1.85	0.12 ± .034
		N = 15

Pacific from California to the Chile-Peru border.

Vertical distribution: Depth data is spotty and no depth rate plot was made, however, data (Appendix B) indicates a depth range of 650 m to at least 1000 m; tropical Pacific maximum net depth figures concur in general with this range.

Geographic variation. Analysis of catches from many widely scattered areas in the Pacific and Indian Ocean gave no indication of population variation (Table 15, Fig. 53). This, coupled with horizontal distribution data, indicates a probable single trans-Indo-Pacific population.

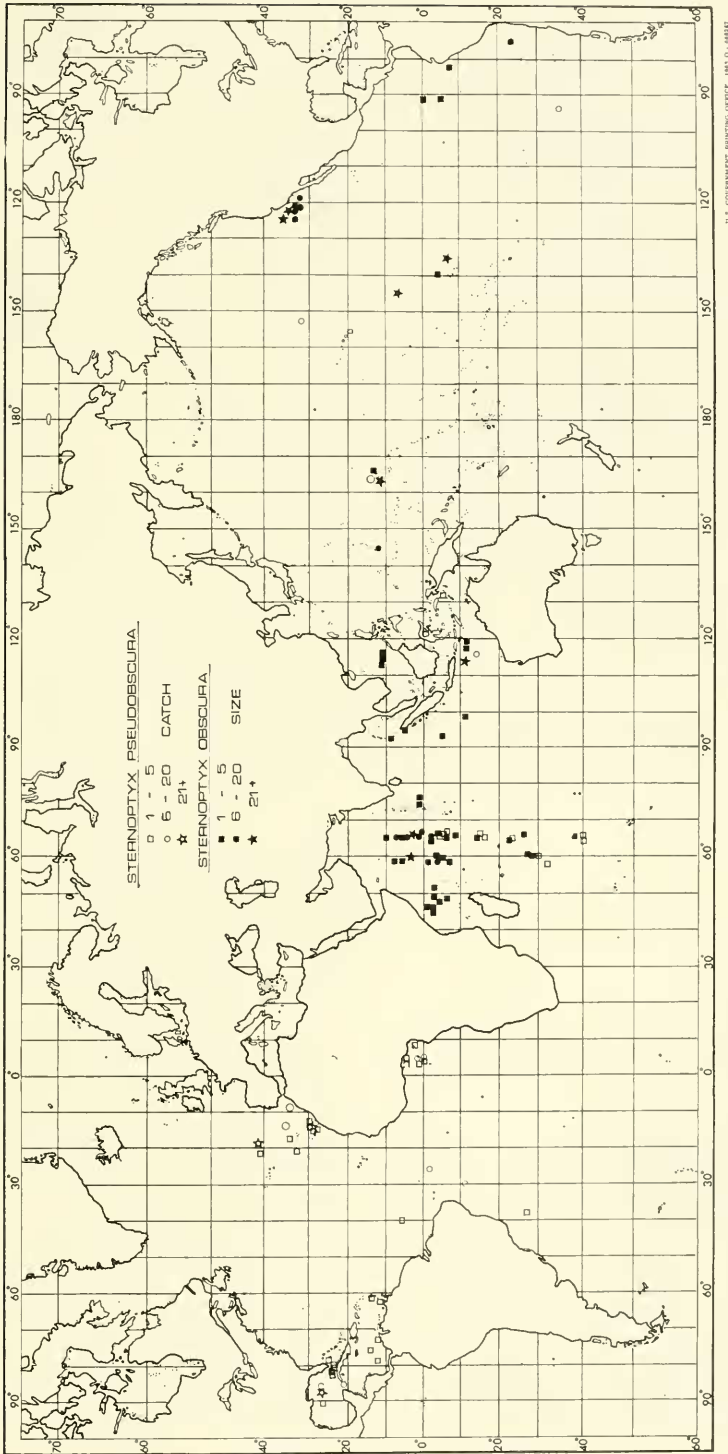


Figure 52. Horizontal distribution of *S. obscura* and *S. pseudobscura*. Catch size categories refer to the number of individuals taken in that haul.

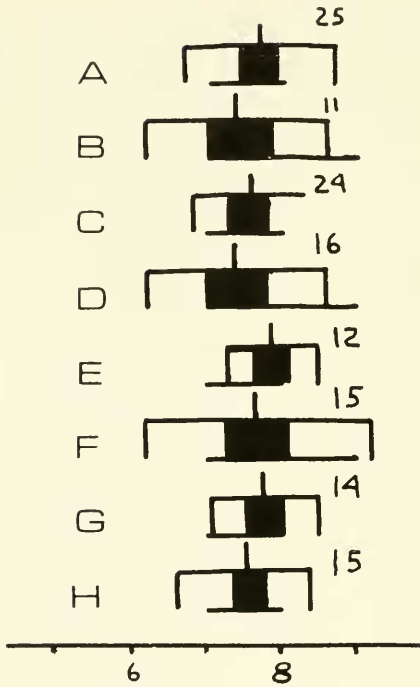


Figure 53. Geographic variation in gill raker count in *S. obscura*. A = E Indian Ocean; B = Central Indian Ocean; C = Tropical E Pacific; D = Banda Sea; E = Central Tropical Pacific; F = Marshall Islands; G = Pacific (California); H = Indian Ocean—S of Bali. Numbers refer to sample size.

Sternoptyx pseudobscura n. sp.
Figure 54

Holotype MCZ 46400, 1° 20'S, 27° 37'W; 2 27/63; R/V CHAIN, Cruise 35; Station 977.
Sternoptyx diaphana: Brauer, 1906: 69 (in part); Maul, 1949b (in part); Blache, 1964: 71; Backus et al., 1965: 139 (in part).

Species distinction. See *S. obscura* (p. 69), differs from *S. diaphana* by its larger mouth (see jaw length, Fig. 62), longer teeth and gill raker tooth plate spines; markedly higher supra-anal photophore; extension of long anal pterygiophores behind and at same level with anal photophores. Tables 18 and 19, and Figures 56, 61, and 62 illustrate the nature and degree of difference between the two species.
Description. D. 10–11; A. 14–16; P. 10–11; total gill rakers 7–9; vertebrae 29.

TABLE 16. REGRESSION STATISTICS FOR VARIOUS POPULATIONS OF *S. PSEUDOBSCURA*.

Character	Regression	
	A	B
<i>Gulf of Guinea</i>		
Jaw length	1.23	0.15 ± .243
Photophore	0.43	0.19 ± .076
		N = 8
<i>Caribbean</i>		
Jaw length	1.70	0.15 ± .045
Photophore	2.28	0.11 ± .052
		N = 13
<i>Florida (30°N, 76°W)</i>		
Jaw length	1.85	0.16 ± .080
Photophore	0.58	0.15 ± .091
		N = 6
<i>Indian Ocean (6°–35°S, 55°–65°E)</i>		
Jaw length	2.04	0.16 ± .200
Photophore	2.21	0.17 ± .098
		N = 6
<i>Central Pacific</i>		
Body depth	–1.06	0.49 ± .078
Abdominal length	0.21	0.32 ± .066
Jaw length	1.63	0.15 ± .061
		N = 13

Largest species in genus, often exceeds 55 mm SL; trunk broad, its depth greater than length; dorsal spine long, its length about equal to, or less than, length of dorsal fin; posterior anal pterygiophores long, extend behind and at same level as anal photophores; supra-anal photophore very high, its height more than one-half the distance from ventral body margin to midline (often raised to midline); no body margin extension in front of anal photophores; jaws large; teeth well developed and recurved; gill raker tooth plates with long spines; usually one much longer than others; anterior dorsal surface of tongue with small nodules; postabdominal and anal pterygiophore spines long; in preservative, pigment dark over most of body except lighter in trunk region; if present, pigment band very narrow at base of caudal rays.

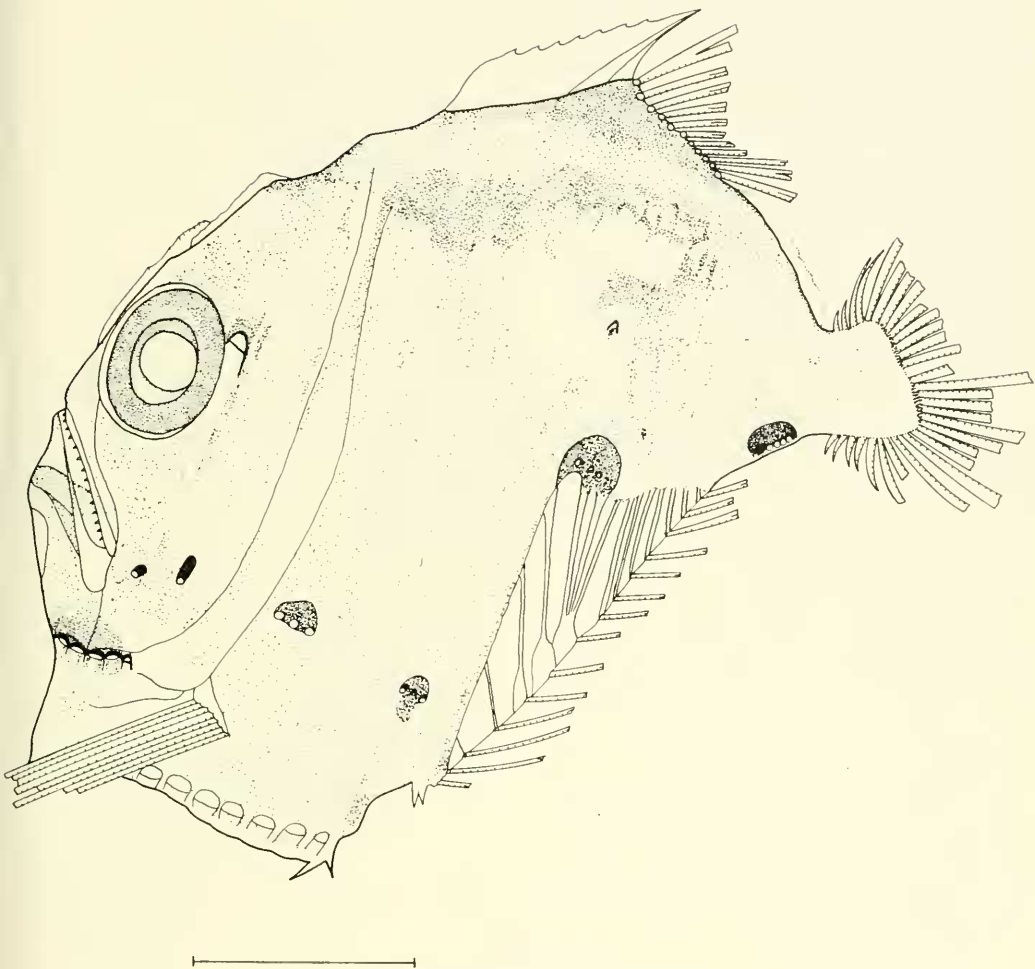


Figure 54. *Sternoptyx pseudobscura*; R/V CHAIN, Cruise 60; Station 1310; 22 mm.

Holotype: measurements (mm), SL 43.1, BD 15.0, JL 07.4, CP 04.6, Ab. length 14.0; meristics: GR 7, D 9, A 15, anal photophores 3; name derivation: *pseudobscura* refers to this species' close resemblance to *S. obscura*.

Distribution. Horizontal distribution (Fig. 52): The limited distributions seen here may be artifacts resulting from the vertical distribution of this species; widely scattered but moderate-to-high catch numbers are additional indications of sampling problems. This species occurs in the South Atlantic off Brazil, and in the Gulf of

Guinea off Africa with widely scattered occurrences in the tropical Atlantic; it is abundant in the northern Gulf of Mexico and the straits of Florida; scattered catches indicate its presence in the southern Caribbean; it has not been reported from the western North Atlantic, but occurs in numbers off the northwest coast of Africa and near the Azores; small catches indicate its presence in the southwestern Indian Ocean from 5°S to 40°S latitude; isolated small-to-moderate catches south of Java, near the Marshall Islands, in the North Pacific, off California, and in the southeast Pacific

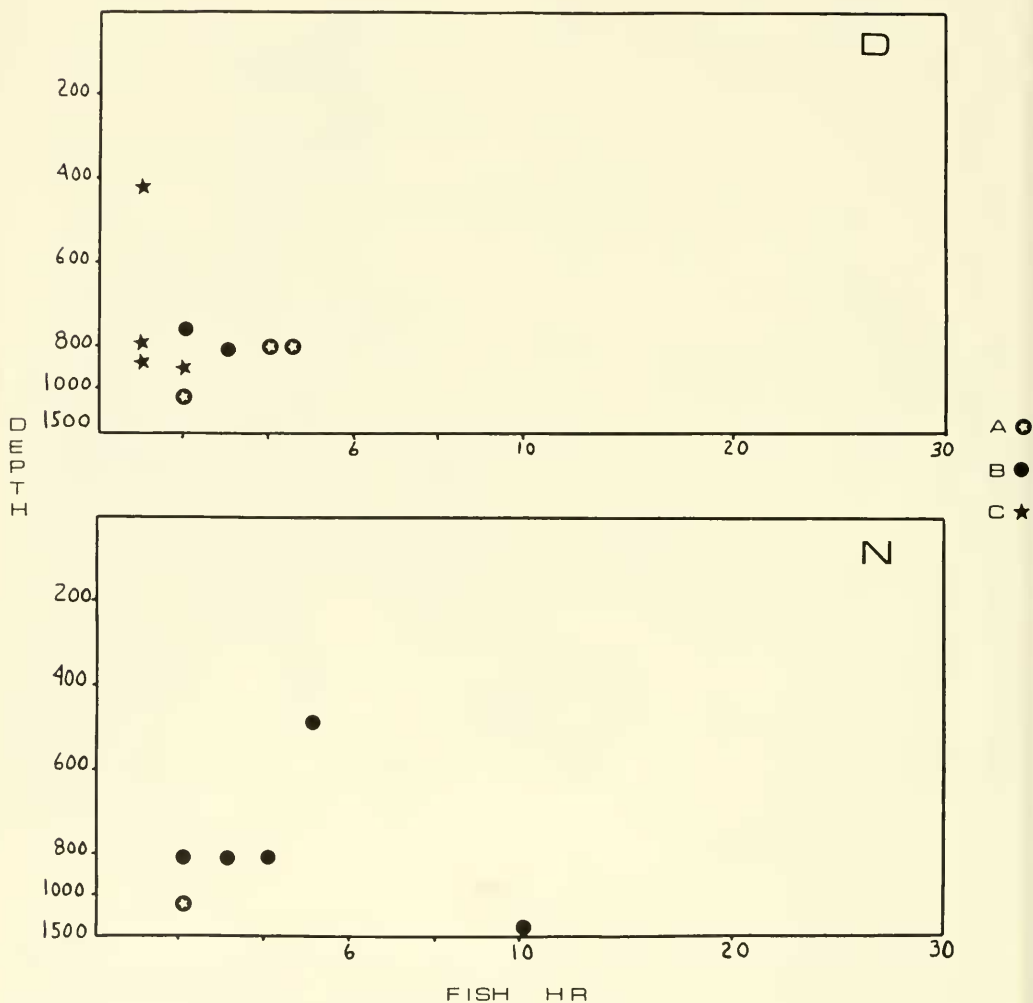


Figure 55. Diurnal vertical distribution of *S. pseudabscura* determined by rate of capture with depth during day (D) and night (N). A = Gulf of Guinea; B = NE Atlantic; C = Gulf of Mexico and Caribbean.

indicate a broad range in the Pacific which future collecting should better define.

Vertical distribution (Fig. 55): The deepest living species in the genus; data indicate a depth distribution from 500 m to 1500 m; greatest concentrations recorded occur between 800 m and 1500 m; overall small rates of capture plus relatively few deep stations may be indicative of a depth preference below 1000 m; no diurnal movement is indicated.

Geographic variation. Small sample sizes, few characters, and the few populations represented precluded a detailed examination of variability in this species. No differences were noted in the Atlantic populations, or in gill raker counts, or jaw length among all populations (Table 16, Fig. 56). The Indian Ocean population could be distinguished from the Atlantic ones by the supra-anal photophore measurement (Fig. 57).

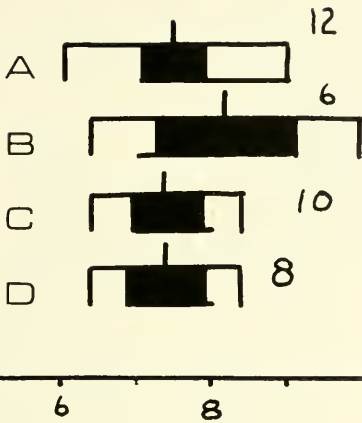


Figure 56. Geographic variation in gill raker count in *S. pseudobscura*. A = Caribbean; B = N Central Pacific; C = Indian Ocean; D = Marshall Islands. Numbers refer to sample size.

Sternoptyx diaphana Hermann

Figure 58

Sternoptyx diaphana Hermann, 1781: 33. In accordance with article 75a(i) Int. Code Zool. Nomen., a neotype is hereby designated: Neotype MCZ 46402; 11° 06'N, 78° 21'W; 8/7/66; R/V ANTON BRUUN, Cruise 19; Station 813. Cuvier and Valenciennes, 1849: 415; Günther, 1864: 387; Goode and Bean, 1896: 127; Alcock, 1896: 331; Gilbert, 1905: 601; Brauer, 1906: 69 (in part); 1908: 175 (eye muscles); Holt and Byrne, 1913: 20; Weber and DeBeaufort, 1913: 1; Jespersen, 1915: 12; Jespersen

and Täning, 1919: 220 (eye); Borodin, 1931: 68; Jespersen, 1934: 15; Roxas, 1934: 287; Buen, 1935: 52; Fowler, 1936: 1208; Beebe, 1937: 22; Parr, 1937: 49; Norman, 1937: 82; 1939: 19; Nybelin, 1948: 25; Maul, 1949a: 17; 1949b: 13 (in part); Wilimovsky, 1951; Misra, 1952: 367; Koumans, 1953: 186; Mead and Taylor, 1953: 570; Smith, 1953: 102; Haig, 1955: 321; Rass, 1955: 328; Grey, 1959: 326; Koefoed, 1961: 11; Schultz, 1961: 617 (in part); 1964: 241 (in part); Backus et al., 1965: 139 (in part); Berry and Perkins, 1965: 682 (in part); Bussing, 1965: 185; Haedrich and Nielsen, 1966: 909; Bright and Paquegnat, 1969: 34.

Species distinction. See *S. obscura* (p. 69) and *S. pseudobscura* (p. 72).

Description. D. 9–11; A. 14–16; P. 10–11; total gill rakers 7–8 (9); vertebrae 29 (30).

Medium size species, seldom exceeds 55 mm SL; trunk very broad; its depth usually greater than its length; dorsal spine long, its length greater or equal to dorsal fin length; posterior anal pterygiophores short, little extension behind and on same level with anal photophores; supra-anal photophore low, not reaching more than one-half the distance from ventral body margin to midline, no body margin extension in front of anal photophores; jaws medium to small; teeth short and low; gill raker tooth plates with low spinate ridges; anterior dorsal

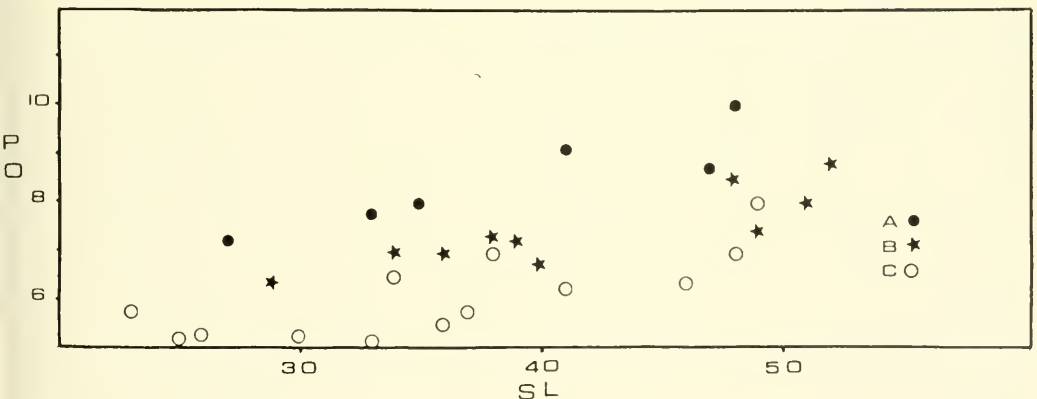


Figure 57. Geographic variation in distance from dorsal body margin of supra-anal photophore (PO) with standard length (SL) in *S. pseudobscura*. A = Indian Ocean; B = Gulf of Guinea; C = Gulf of Mexico and Caribbean.

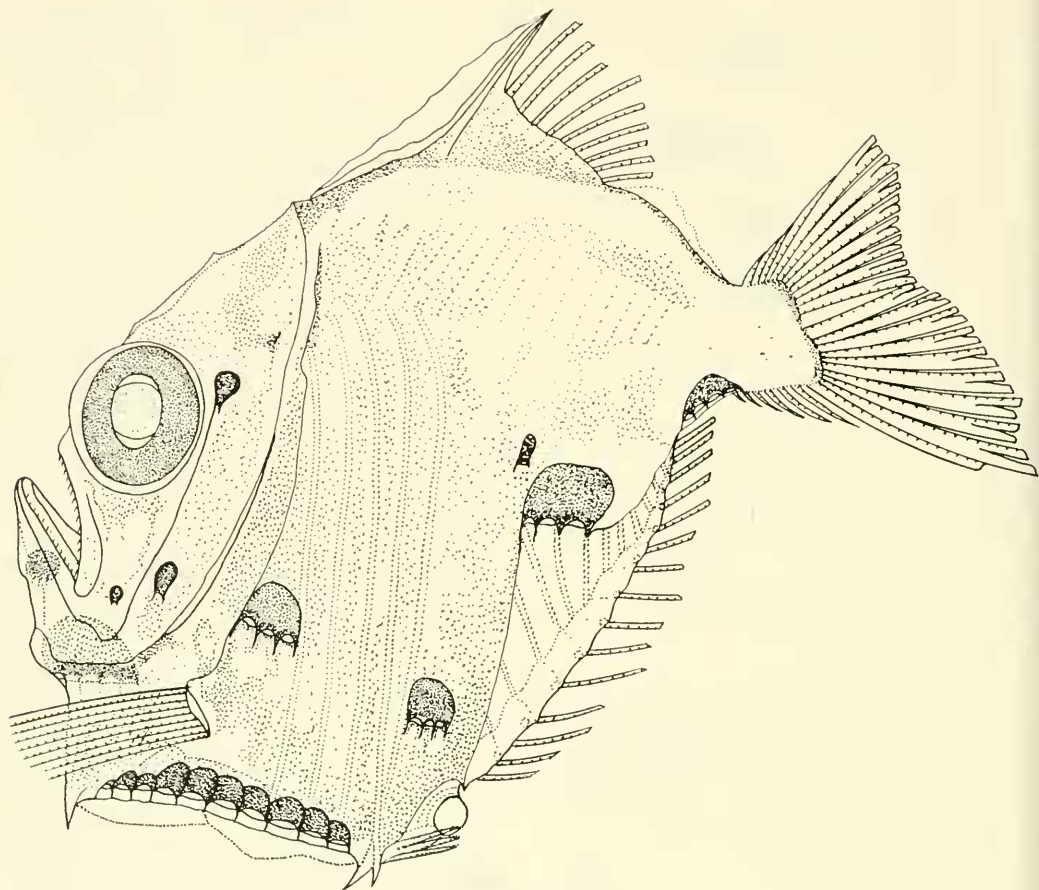


Figure 58. *Sternaptyx diaphana*; GALATHEA; Station 494; 33 mm.

surface of tongue with small nodules; post-abdominal and anal pterygiophore spines usually shorter than others in genus; in preservative pigment dark dorsally, often light and dispersed in trunk region, usually little pigment present at base of caudal rays.

Neotype: measurements (mm): SL 28.4, BD 12.1, JL 05.3, CP 03.5, Ab. length 09.0; meristics: GR 7, D 10, A 15, anal photophores 3.

Distribution. Horizontal distribution (Fig. 59): Broadly distributed in the Atlantic, caught in moderate numbers in the South Atlantic off Brazil and from 20°W to the African coast at about 35°S; abundantly

present in the Gulf of Guinea and the tropical Atlantic; taken abundantly in the southern Caribbean, the Gulf of Mexico, and straits of Florida; taken in the western North Atlantic; a large population occurs in the northeastern Atlantic from 25°N to 45°N latitude. In the western Indian Ocean small to moderate catches extend from 5°S to 35°S latitude, a single catch has been observed from the eastern Indian Ocean; numerous catches indicate this species present south of Java, near Borneo, and in the Banda Sea; known also between New Guinea and the Solomon Islands, it occurs in the western Pacific near the Philippines and along the coast of Japan, with a small

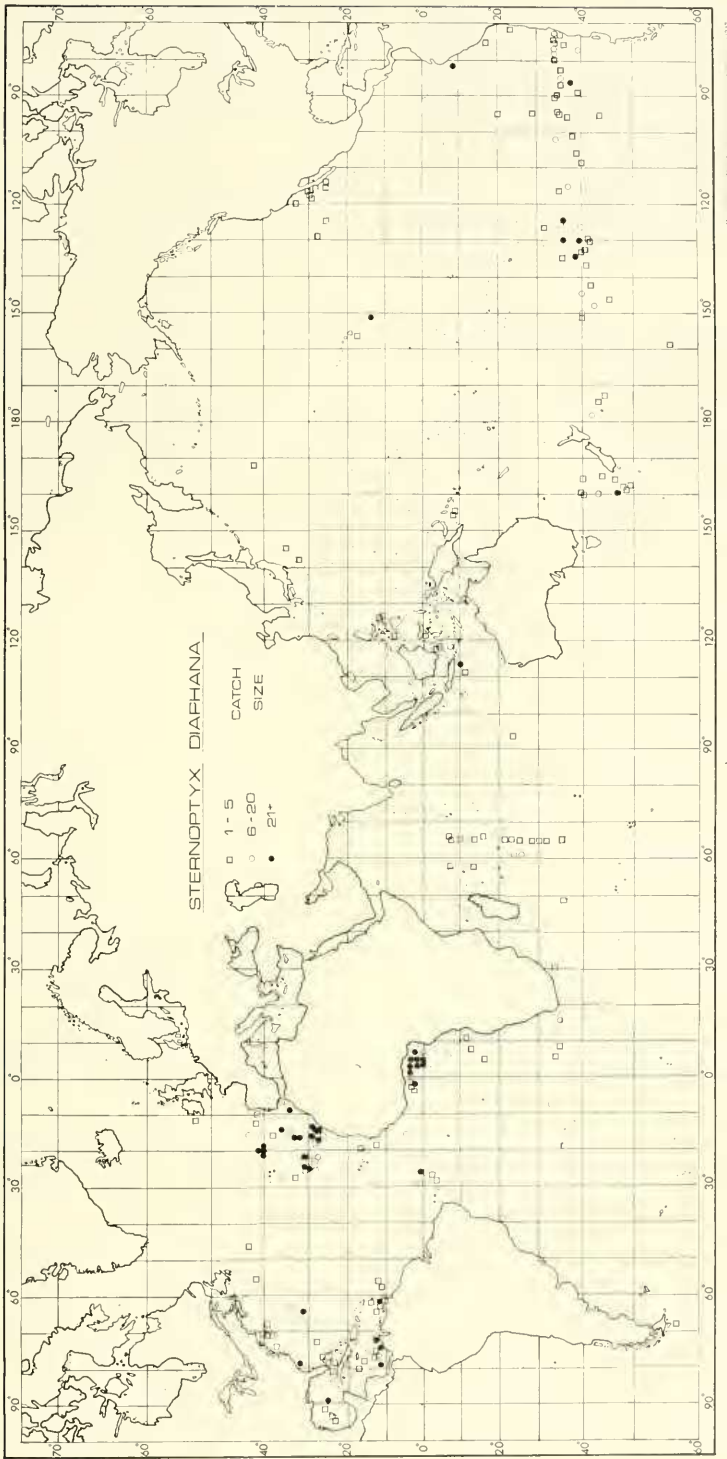


Figure 59. Horizontal distribution of *S. diaphana*. Catch size categories refer to the number of individuals taken in that haul.

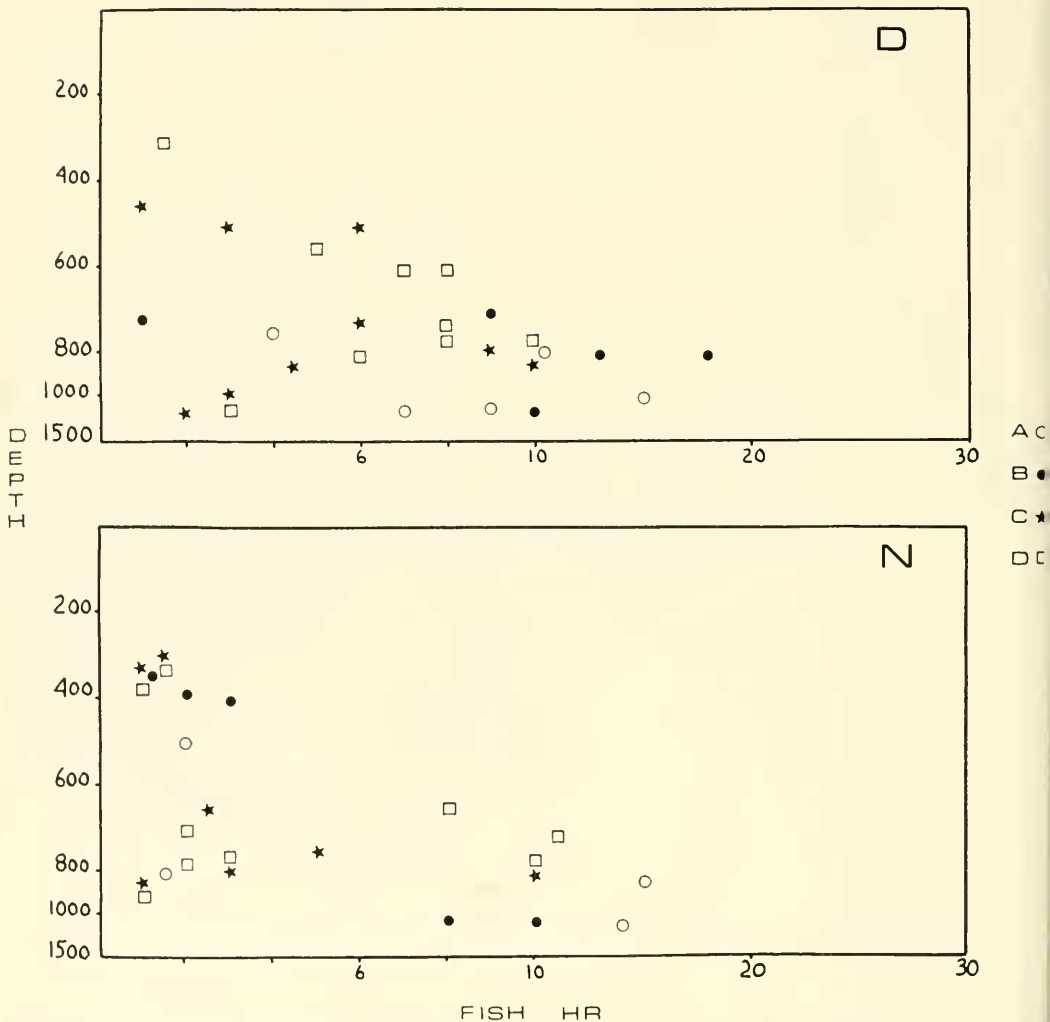


Figure 60. Diurnal vertical distribution of *S. diaphana* determined by rate of capture with depth during day (D) and night (N). A = Southern Ocean; B = Gulf of Guinea; C = Gulf of Mexico and Caribbean; D = NE Atlantic.

sample taken in the North Pacific; this species occurs in small numbers off lower California and has been reported abundantly southeast of Hawaii; a large population extends across the South Pacific from Chile to about 160°E longitude.

Vertical distribution (Fig. 60): Distributed between 400 m and 1200 m; major concentrations occur between 700 m and 900 m; no diurnal movement or marked

geographical depth variation could be detected.

Geographic variation. With the exception of the Pacific southern ocean population, little geographic variation could be detected; characters were few and sample sizes small, however (Table 17, Fig. 61). The Southern Ocean population is quite distinct and certainly represents an instance of incipient speciation. Tables 1'

TABLE 17. REGRESSION STATISTICS FOR VARIOUS POPULATIONS OF *S. DIAPHANA*.

Character	Regression	
	A	B
<i>Caribbean</i>		
Jaw length	-0.24	$0.18 \pm .066$
Photophore	-2.04	$0.37 \pm .101$
		N = 11
<i>Java (10°S, 114°E)</i>		
Body depth	-2.93	$0.54 \pm .107$
Abdominal length	0.78	$0.31 \pm .056$
		N = 22
<i>Indian Ocean (5°-40°S, 55°-65°E)</i>		
Body depth	0.10	$0.51 \pm .095$
Abdominal length	1.18	$0.31 \pm .093$
Photophore	0.20	$0.29 \pm .085$
Jaw length	1.00	$0.15 \pm .088$
		N = 12
<i>Southern Ocean</i>		
Body depth	-0.77	$0.42 \pm .044$
Abdominal length	1.18	$0.31 \pm .093$
Jaw length	1.47	$0.16 \pm .041$
Photophore	2.23	$0.11 \pm .033$
		N = 40
<i>Southern Ocean (Chile)</i>		
Body depth	-1.50	$0.41 \pm .113$
Jaw length	1.46	$0.14 \pm .037$
		N = 11

and 18 indicate the degree of difference between this population and others in the species. In body depth it falls somewhat between most populations of *S. diaphana* and *S. obscura* (Table 19). Phenotypically it has supra-anal photophore characteristics

resembling some populations of *S. pseudobscura*. In most characters it falls closest to other populations of *S. diaphana*, especially in mouth and gill raker characteristics. Considering the lack of sympatry with other forms and the degree of distinctness between the species, it is presently considered to represent a distinct form of *S. diaphana*.

Genus *Polyipnus* Günther, 1887

Polyipnus Günther, 1887: 170 (type species: *Polyipnus spinosus* Günther, 1887, by monotypy).

Diagnosis. Ten abdominal, three supra-abdominal, and a lateral photophore; post-temporal spine(s) well developed; a fused double dorsal pterygiophore forms short spines anterior to dorsal fin rays; cleithrum projects below pectoral fin forming fanlike, spine-bearing extension posteriorly; otoliths very large with characteristic armlike extension (see Kotthaus, 1967); three to four hypural elements in upper caudal lobe; lower jaw noticeably expanded dorsally.

Description. Photophores: PO 1; PTO 1; BR 6; I 6; PRO 1; SO 1; SP 3; SAB 3; AB 10; L 1; PAN 5; AN 6-14; SC 4.

Spines: Post-temporal extends posteriorly to form from one to three prominent spines; preopercle spined, the lateral surface often bearing spiny elements; retro-articular spined; ventral surface of lower jaw often serrate; cleithrum bears pre-abdominal spine; bony keel scales often bear spines ventrally; four postabdominal

TABLE 18. SLOPE COMPARISONS BETWEEN REGRESSIONS OF SEVERAL CHARACTERS IN SPECIES OF *STERNOPTYX*. D = *S. DIAPHANA*; O = *S. OBSCURA*; P = *S. PSEUDOBSCURA*.

Character	Population 1	Population 2	T	P
Body depth	Java D	Java O	2.780	.001
	Central Pacific P	Central Pacific O	2.362	.025
	Java D	Southern Ocean D	2.611	.010
Abdominal length	Java D	Southern Ocean D	2.381	.023
Photophore	Caribbean P	Caribbean D	4.977	.001
	Gulf of Guinea P	Caribbean D	3.240	.005
	Florida P	Caribbean D	2.767	.018

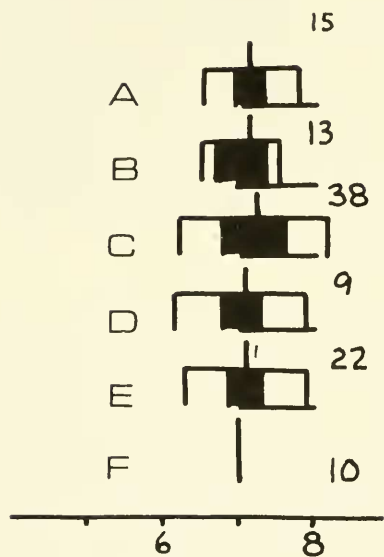


Figure 61. Geographic variation in gill raker count in *S. diaphana*. A = Caribbean; B = Indian Ocean; C = Southern Ocean; D = Pacific (Chile); E = Indian Ocean—S of Bali; F = Java Sea. Numbers refer to sample size.

spines; first anal pterygiophore may extend ventrally to form small spines.

Eyes: Large, well developed, nonteleoscopic, essentially laterally oriented.

Gill rakers: Number 10–28; well developed, long, often quite close together; first branchial arch considerably larger

than succeeding arches; the inner surfaces of second and third cerato- and epi-branchials bear tooth plates.

Jaws and dentition: Mouth small and vertically oriented; premaxilla long toothed, and major upper jaw bone in gape; arm of first supramaxilla elongate; dorsal margin of lower jaw greatly expanded which, with broadening in the meso- and metapteryoid, make the mouth cavity a long conelike basket with a substantial distance between the mouth entrance and the beginning of the branchial arches; the maxilla is toothed, but essentially excluded from gape; teeth small to minute, no canines, vomer and palatines bear teeth.

Meristics: Vertebrae 31–36; C. 9+10; D. 10–17; A. 13–19.

Color: Bright silvery in life; dark dorsal pigment band often extends ventrally and may reach lateral midline; dark pigment may form lateral striated bands on posterior trunk.

Internal anatomy: Swim bladder and associated gland well developed, gland quite large, with grainy appearance; bladder thick walled, and often heavily invested with fatty tissue (see Marshall, 1960); digestive system simple with bipartate stomach, anterior section thick walled, the lining often raised into heavy

TABLE 19. COMPARISONS BETWEEN MEAN SLOPES OF SEVERAL CHARACTERS AMONG THE SPECIES OF *STERNOPTYX*. S.O. = SOUTHERN OCEAN POPULATIONS OF *S. DIAPHANA*; POP. # = NUMBER OF POPULATIONS; \bar{x} SLOPE = UNWEIGHTED MEAN SLOPE; TOTAL # = TOTAL NUMBER OF FISH MEASURED OVER ALL POPULATIONS.

Species	Character	Pop. #	\bar{x} Slope	Range	Total #
<i>S. obscura</i>	body depth	6	0.32	0.27–0.37	104
<i>S. diaphana</i>	body depth	2	0.525	0.51–0.54	34
<i>S. diaphana</i> (S.O.)	body depth	2	0.415	0.41–0.42	51
<i>S. pseudobscura</i>	body depth	1	0.49	0.49	13
<i>S. diaphana</i>	photophore	4	0.31	0.29–0.37	35
<i>S. diaphana</i> (S.O.)	photophore	1	0.11	0.11	40
<i>S. pseudobscura</i>	photophore	4	0.15	0.11–0.18	33
<i>S. obscura</i>	jaw length	4	0.13	0.09–0.15	56
<i>S. diaphana</i>	jaw length	5	0.196	0.15–0.23	41
<i>S. diaphana</i> (S.O.)	jaw length	2	0.15	0.14–0.16	51
<i>S. pseudobscura</i>	jaw length	5	0.15	0.15–0.16	46

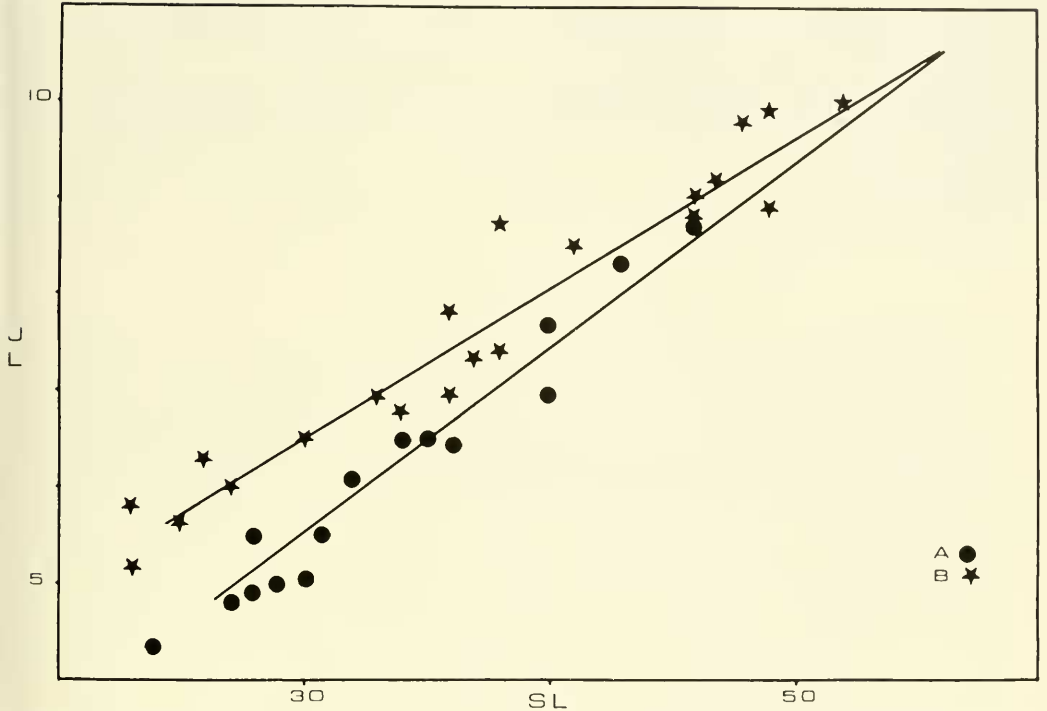


Figure 62. Regression of lower jaw length (JL) on standard length (SL) in *S. diaphana* (A) and *S. pseudobscura* (B) from the Tropical Atlantic.

ridged folds; the posterior section thin walled and extensible, six to ten pyloric caecae, short straight intestine, and a relatively large well-developed liver. Gonads, when mature, lie horizontally and laterally in the body cavity; cavity lined with pigmented membrane; nephritic tissue is not as well developed as in other genera.

Species complexes: As with *Argyropelecus*, there has been considerable radiation within the genus. There are three distinct species complexes, two closely related. The third complex, *P. spinosus*, is quite distinct. The latter appears more primitive in terms of axial and caudal skeleton characteristics. The *P. spinosus* complex differs from the other two groups as follows: greater development of the post-temporal spine complex; otoliths (Weitzman, personal conversation); four hypural elements in the upper caudal lobe; serrate lower jaw mar-

gin; spine-bearing abdominal keel plates; the second and third preterminal neural spines wedge shaped; extension of the cleithrum below the pectoral relatively more broadened; and the anal pterygiophore gap is reduced.

Within the *P. spinosus* complex there is a further dichotomy. *P. nuttingi*, *P. oluolus*, and *P. indicus* with peculiar reductions in post-temporal spine characteristics, form one group; *P. spinosus*, *P. sterope*, and *P. tridentifer* with a well-developed, post-temporal complex, form the other.

The *P. asteroides* and *P. laternatus* species complexes are more closely related. They differ primarily in post-temporal spine characteristics, body shape and size, photophore number and pattern, and dentition. Both complexes have similar otoliths and resemble each other osteologically.

The species *P. laternatus*—*P. omphus*

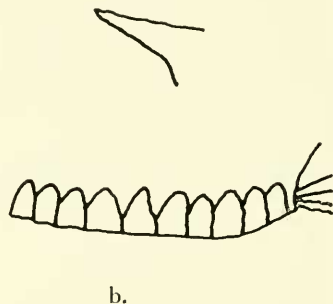
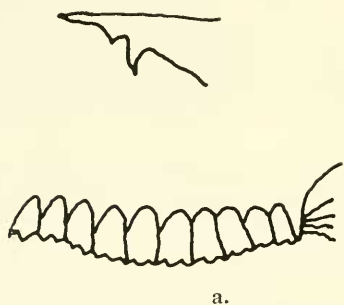
and *P. unispinus*—*P. aquavitus* form a dichotomy within the *P. laternatus* complex. The differences include preopercle spine length, body shape, photophore pattern, and some meristic differences (gill rakers, vertebral number).

P. asteroides—*P. polli*—*P. triphanos* and *P. matsubarae*—*P. meteori*—*P. kiwiensis*—*P.*

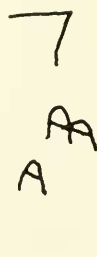
ruggeri form a similar dichotomy within the *P. asteroides* complex. The latter group is characterized by an extremely long, narrow, posterior vomerine shaft, closely allied and fitting into the parasphenoid. This shaft bears teeth anteriorly, in addition to the normal lateral vomerine teeth. Other minor differences are also present.

KEY TO THE SPECIES OF *Polyipnus*

- 1a. Post-temporal spine complex, bearing one or two basal supplementary spines; dorso-lateral edge of fused, post-temporal-supracleithrum serrate; abdominal keel scales with spiny ventral surfaces; supra-anal photophore group usually not distinctly separated from anal group *P. spinosus* complex 3
- b. Post-temporal spine simple, bearing no basal spines; lateral edge of post-temporal-supracleithrum smooth; keel scales with smooth ventral surfaces (except *P. unispinus*); supra-anal photophores separate, usually raised well above anal group 2



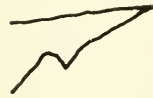
- 2a. Post-temporal spine long, its length greater than one-fourth the diameter of orbit; anal photophore number 10 to 13 (adults only); body long and narrow, SL greater than 1.7 times body depth; first supra-anal photophore even with or raised above the second (except *P. laternatus* in which the first is slightly lower than the second) *P. laternatus* complex 8
- b. Post-temporal spine short, its length less than one-fourth the diameter of orbit; anal photophore number 7 to 9 (occasionally 10); body more robust, SL less than 1.9 times body depth; first supra-anal photophore markedly lower than second *P. asteroides* complex 11



- 3a. Post-temporal spine with two distinct basal spines; anal-subcaudal photophore distance less than one-third the length of the subcaudal group; anal photophore number 10 to 13 4
- b. Post-temporal spine with a single distinct basal spine (this reduced in *P. oluolus*); anal-subcaudal distance greater than one-half of the length of the subcaudal group; anal photophore number 6 to 9 6



a.



b.

- 4a. Anal photophore number 10; SL less than 3.6 times body depth at end of dorsal fin; caudal peduncle broad, head length less than 2.8 times narrowest peduncle depth 5
- b. Anal photophore number 12 to 13; SL greater than four times body depth at end of dorsal; caudal peduncle narrow, head length greater than three times narrowest peduncle depth *P. tridentifer* (p. 86).
- 5a. Post-temporal basal spines well developed, ventralmost basal spine length greater than one-half length of post-temporal spine; gill raker number 24–28 *P. sterope* (p. 88).
- b. Post-temporal basal spines short, ventralmost basal spine less than one-fourth post-temporal spine length; total gill raker number 18 to 21 *P. spinosus* (p. 89).

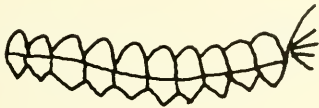


a.

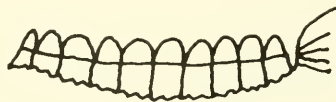


b.

- 6a. Abdominal keel scales triangulate, with one or two large ventral spines; post-temporal spine long, heavily spinose dorsally and laterally; first supra-anal photophore markedly lower than third; anal photophores 6 to 7 *P. oluolus* (p. 90).
- b. Abdominal keel scales rectangular, with many small ventral spines; post-temporal spine long and smooth or short and spinose dorsally only; first supra-anal photophore about even with or raised above third; anal photophores 8 to 9 7



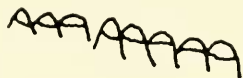
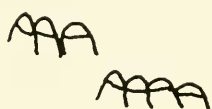
a.



b.

- 7a. Ventral margin of subcaudal photophores with spines (adults); anal-subcaudal photophore distance less than three-fourths length of subcaudal group; first supra-anal photophore higher than the last; post-temporal spine long, greater than one-half diameter of orbit *P. indicus* (p. 91).
- b. Ventral margin of subcaudal photophores smooth; anal-subcaudal distance greater than three-fourths length of subcaudal group; first supra-anal photophore lower than last; post-temporal spine short, less than one-half diameter of orbit *P. nuttingi* (p. 92).

- 8a. Gill rakers 18 to 21; supra-anal photophores distinctly raised above the anal group; preopercle spine short, somewhat triangulate 9
- b. Gill rakers 12 to 14; supra-anal photophores not markedly raised above anal group; preopercle spine long and slender 10

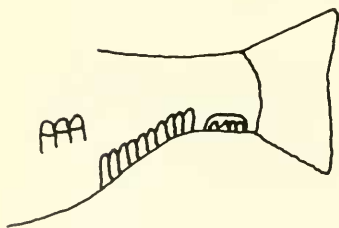


a.

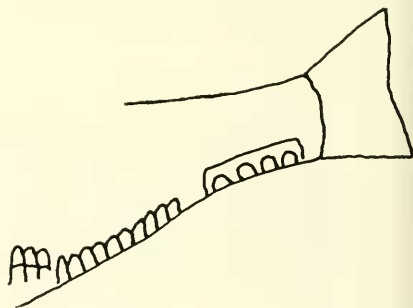


b.

- 9a. Subcaudal photophores compact, length of subcaudal group less than narrowest caudal peduncle depth; distance from top of last supra-anal photophore to top of first anal greater than three-fourths length of preanal group *P. lateruatus* (p. 92).
- b. Subcaudal photophores somewhat spread; length of subcaudal group equal or greater than narrowest peduncle depth; distance from top of last supra-anal photophore to top of first anal less than one-half preanal length *P. omphus* (p. 94).

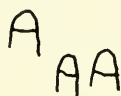


a.

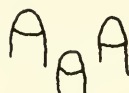


b.

- 10a. Posterior lateral margin of preopercle smooth; ventral keel scales smooth; dorsal spine short, length less than one-fourth diameter of orbit *P. aquavitus* (p. 96).
- b. Posterior lateral margin of preopercle serrate; ventral edge of keel scales with small spinelets; dorsal spine long, length greater than one-half diameter of orbit *P. uisipinus* (p. 97).
- 11a. Teeth absent on posterior vomerine shaft; second supra-anal photophore even with or raised above third; supra-abdominal photophores nonsymmetrical, first photophore raised well above other two 12
- b. Teeth present on posterior vomerine shaft; second supra-anal photophore lower than third; supra-abdominal photophores symmetrical, first not markedly raised above third 14



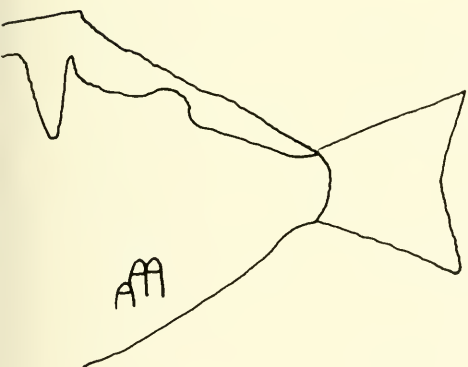
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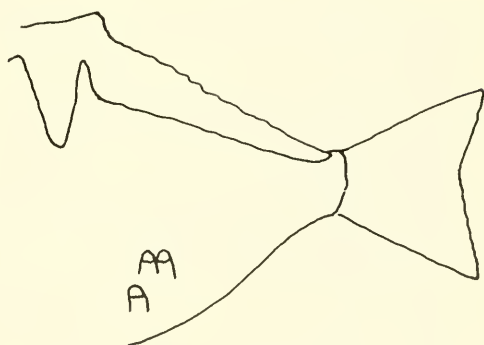
b.

12a. Gill rakers 16 to 18; dorsal rays 11 to 12; lower margin of dark dorsal pigment markedly raised above supra-anal photophores *P. triphanos* (p. 97).

b. Gill rakers 20 to 24; dorsal rays 14 to 16; lower margin of dark dorsal pigment straight from dorsal spine to caudal peduncle 13



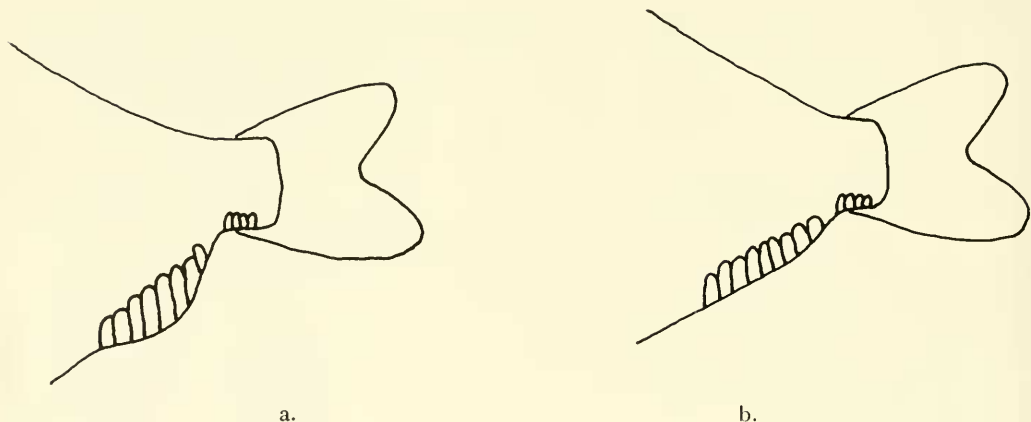
a.



b.

13a. Anal pterygiophores form circular margin below anal photophores; anal photophores number 7 to 8; SL less than 3.5 times body depth at end of dorsal — *P. polli* (p. 98).

b. Anal pterygiophore margin essentially straight; anal photophore number 9 (rarely 10); SL greater than 3.7 times body depth at end of dorsal — *P. asteroides* (p. 99).



- 14a. Gill rakers 22 to 24; dark pigment bar extending to midline very narrow, its width less than greatest width of lateral photophore (see illustration p. 101) *P. matsubarae* (p. 101).
 b. Gill rakers 13 to 18; dark pigment bar absent or much wider than width of lateral photophore 15
- 15a. Dark pigment bar greatly reduced or absent; supra-abdominal photophores essentially in straight line (see illustration p. 102); gill rakers 18 *P. ruggeri* (p. 102).
 b. Dark pigment bar present, extending to midline; supra-abdominal photophores tri-angulate, the second markedly lower than the other two; gill rakers 13 to 17 16
- 16a. Gill rakers 13 to 15; light stripe behind dark pigment bar extends to mid-dorsal line; ventral border of dark dorsal pigment markedly raised above supra-anal photophores (taken from photo and description, Kotthaus, 1967) *P. meteori* (p. 104).
 b. Gill rakers 16 to 17; light stripe behind dark pigment bar not extending to mid-dorsal line; ventral border of dark dorsal pigment not markedly raised above supra-anal photophores (see illustration p. 103) *P. kiucensis* (p. 103).

Polyipnus tridentifer McCulloch

Figure 64

Polyipnus tridentifer McCulloch, 1914: 78 (lecto-type AM E3543; designation Schultz, 1961; Australian Bight; not seen); Schultz, 1961: 619; 1964: 247.

Polyipnus spinosus: Weber and DeBeaufort, 1913: 1; Matsubara, 1950: 192; Okada and Suzuki, 1956: 297; Suzuki, 1964: 1.

Polyipnus frazeri Fowler, 1933: 257; Schultz, 1961: 620.

Species distinction. Differs from *P. spinosus* and *P. sterope* in its long, narrow trunk and caudal peduncle; long, smooth post-temporal spine; more sharply angled dorsal spine; multispinose subcaudal scales; less spinose abdominal keel scales; differs from *P. spinosus* by its much longer third basal post-temporal spine.

Description. D. 13–14; A. 15–17; P. (12) 13–14; total gill rakers (20) 21–24; vertebrae 33–34.

Medium size species, not often exceeding 60 mm SL; trunk tapering into long, narrow, caudal peduncle; its depth less or equal to length of subcaudal photophore group; post-temporal spine long, its length more than one-half the distance from its base to point of dorsal spine; second basal post-temporal spine long; dorsal surface of post-temporal spine relatively smooth, lacking marked serrations; supra-abdominal photophores arranged in steplike fashion, each raised an approximate equal distance above the next; abdominal keel scales spinose, although spines very short; scales below subcaudal photophores with several prominent spines; preopercle spine di-

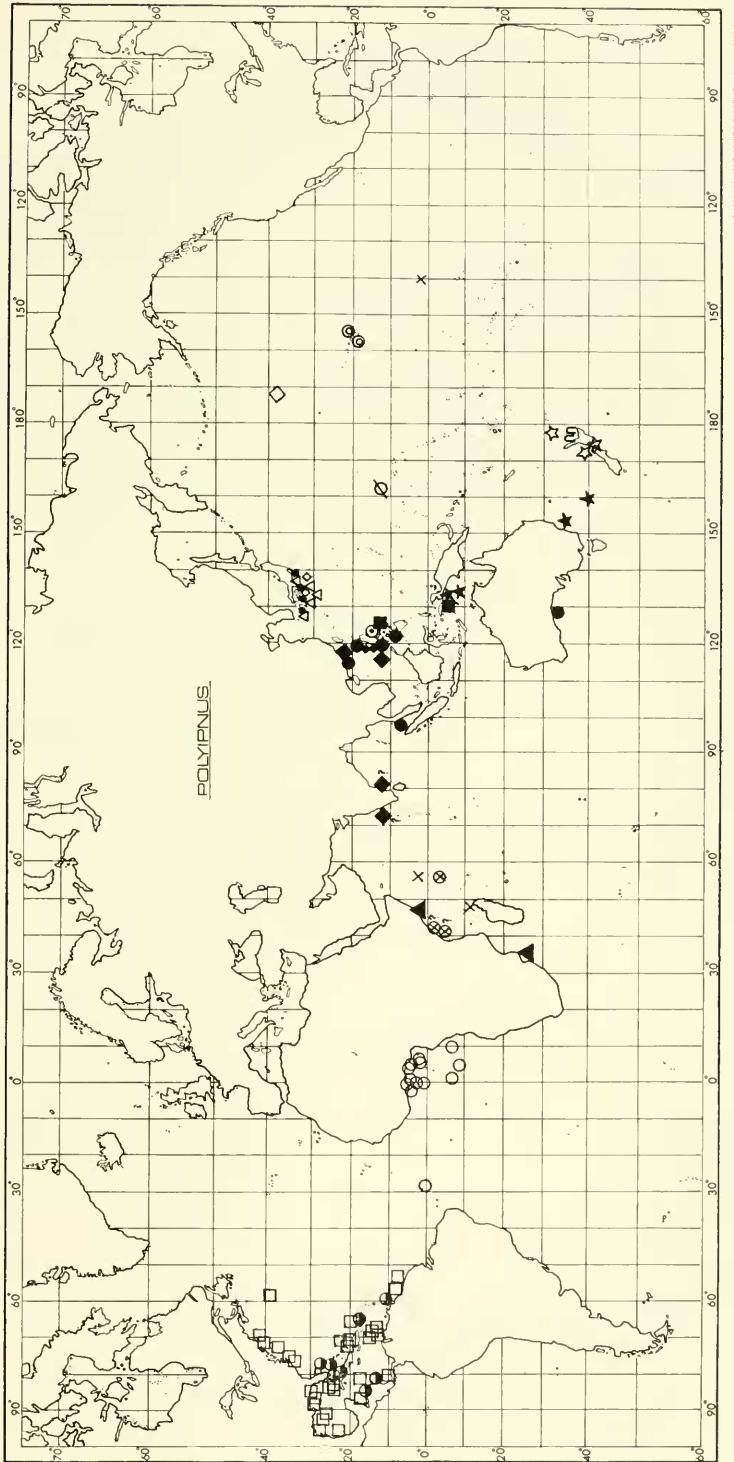


Figure 63. The distribution of the genus *Polyipnus*. Species: ● *P. spinosus*; ● *P. tridentifer*; ⊗ *P. oluolus*; □ *P. lateratus*; □ *P. asteroides*; ○ *P. polli*; X *P. omphus*; ⊗ *P. meteori*; ▲ *P. indicus*; ◆ *P. unispinus*; ★ *P. aquavitus*; ★ *P. ruggeri*; □ *P. kiwiensis*; △ *P. sterope*; ◇ *P. matsubarai*; ⊗ *P. nuttingi*; ⊗ *P. nuttingi*.

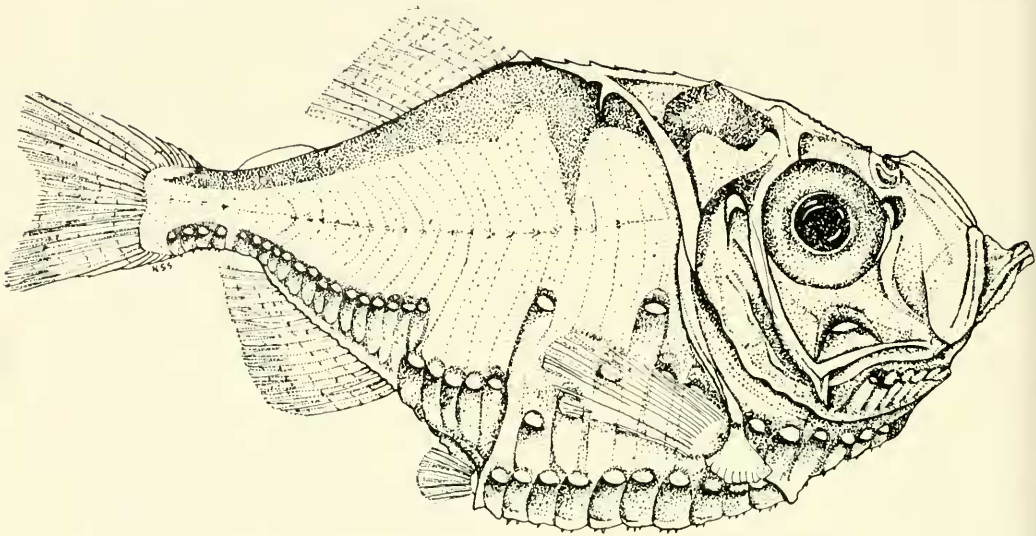


Figure 64. *Polyipnus tridentifer*; after Matsubara, 1950.

rected, at its base, posteriorly, curving distally to point ventrally or slightly anteriorly; jaws medium; teeth minute; gill rakers long; pigment in preservative dark dorsally with narrow, dark bar extending toward midline; pigment diffuse on trunk.

Distribution (Fig. 63). Restricted to the western Pacific, taken abundantly around the Philippines, off the south China coast, off Japan, in waters north of the Strait of Malacca, and in the Great Australian Bight.

Polyipnus sterope Jordan and Starks

Figure 65

Polyipnus sterope Jordan and Starks, 1904: 581 (holotype USNM 51451; Sagami Bay, Japan: seen); Matsubara, 1941: 2; Haneda, 1952: 12 (light organs); Okada and Suzuki, 1956: 297; Suzuki, 1964: 1 (X-ray).

Polyipnus spinosus: Kamohara, 1952: 17.
Polyipnus spinosus sterope Schultz, 1961: 621; 1964: 247.

Species distinction. See *P. tridentifer*

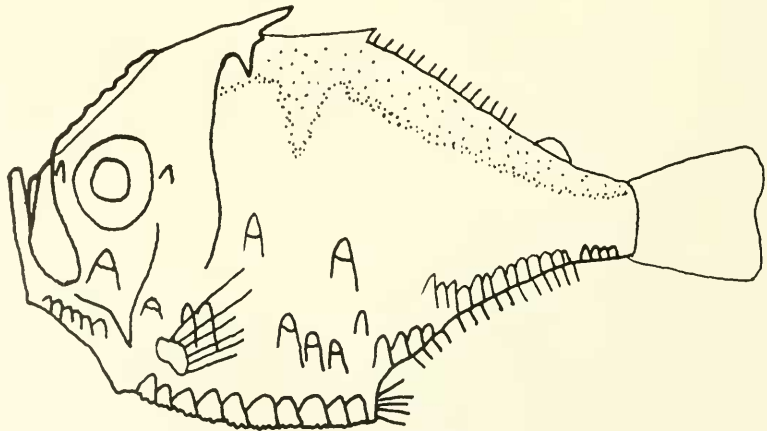


Figure 65. *Polyipnus sterope*; modified from Jordan and Starks, 1904.

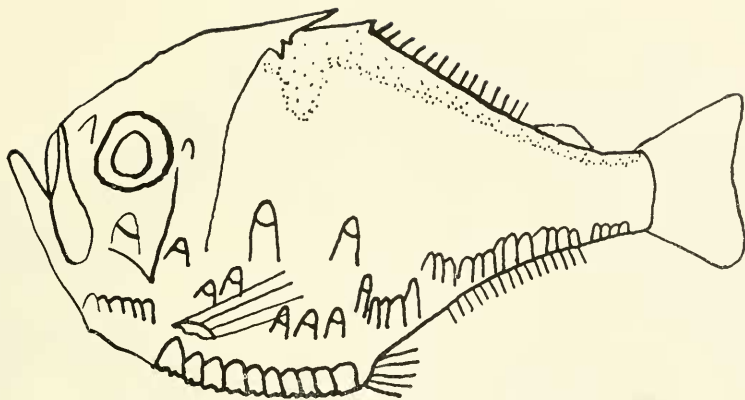


Figure 66. *Polyipnus spinosus*; modified from Günther, 1887.

(p. 86); differs from *P. spinosus* in its longer basal post-temporal spines; shorter preopercle spine; more raised first supra-abdominal photophore, somewhat shorter post-temporal spine in relation to its base-to-dorsal spine length, and higher gill raker count.

Description. D. 13–14; A. 15–17; P. 13–15; total gill rakers (23) 24–28; vertebrae 33–34.

Medium to large species, seldom exceeding 70 mm SL; trunk broadly tapering; caudal peduncle broad, its depth more than length of subcaudal photophore group; post-temporal spine spinose dorsally, its length substantially less than one-half distance from its base to point of dorsal spine; third basal post-temporal spine long, second basal spine prominent; dorsal spine high, with flangelike anterior portion not rising sharply from dorsal surface; supra-abdominal photophores positioned in a step-wise arrangement, with first photophore raised above other two; abdominal keel scales very spinose, including those ventral to preanal photophores; subcaudal scales either smooth or with single short spine; jaws medium; gill rakers long; preopercle spine curves slightly anteriorly; pigment in preservative dark dorsally with very narrow bar extending toward midline; pigment diffuse on trunk.

Distribution (Fig. 63). Known only from the waters around Japan, where it has been taken less abundantly than *P. tridentifer*.

Polyipnus spinosus Günther

Figure 66

Polyipnus spinosus Günther, 1887: 170 (holotype BMNH, East Indies; not seen); Alcock, 1896: 331; 1899: 135; Brauer, 1906: 69 (larvae, fig.) (in part); 1908: 175 (eye muscles); Roxas, 1934: 287; Misra, 1952: 367; Koumans, 1953: 186 (?); Samuel, 1963: 101 (?).

Polyipnus spinosus spinosus Schultze, 1961: 624; 1964: 247.

Species distinction. See *P. tridentifer* (p. 86) and *P. sterope* (p. 88).

Description. D. 13–14; A. 15–17; P. 13–15; total gill rakers 18–21; vertebrae 33–34.

Medium to small species, seldom exceeding 70 mm SL; trunk and caudal peduncle broad, its depth greater than or equal to length of subcaudal photophore group; post-temporal spine spinose dorsally, its basal spines reduced; post-temporal spine nearly equal to one-half the distance from its base to dorsal spine; dorsal spine similar to *P. sterope*; supra-abdominal photophore positioned with first photophore only slightly raised above other two; first two supra-anal photophores slightly raised from third; preopercle spine long, curving anteriorly; abdominal and preanal keel scales

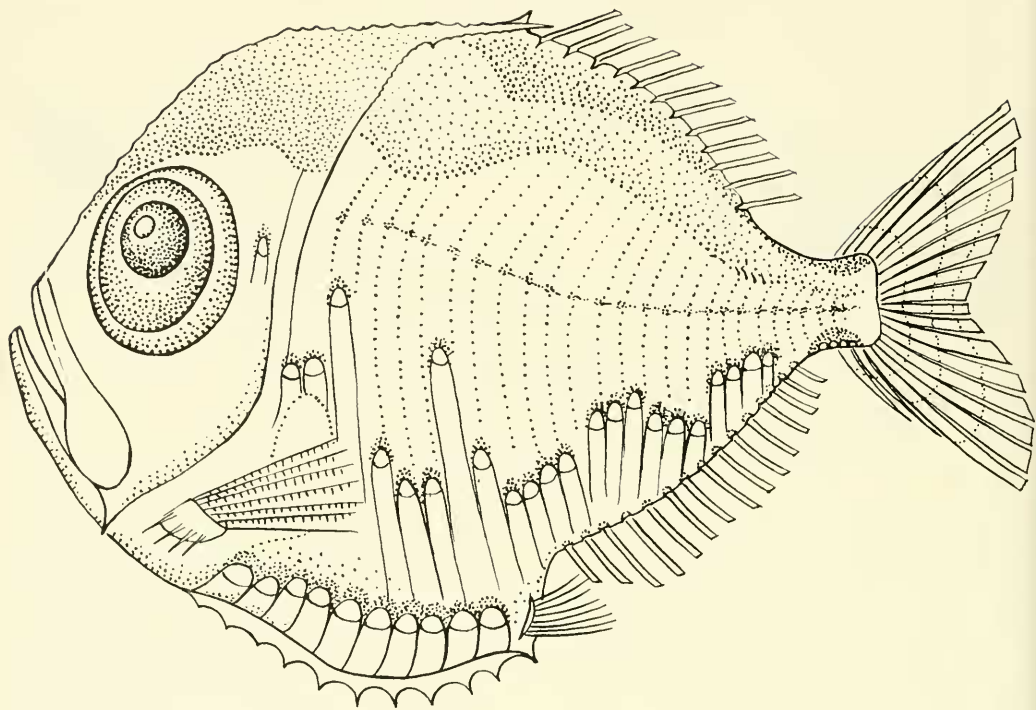


Figure 67. *Polyipnus oluolus*; R/V HUGH M. SMITH, Cruise 37; Station 43; SL 33 mm.

spinose; subcaudal scales with no spines to a single small spine; jaws medium; gill rakers long; pigment in preservative dark dorsally, with narrow dark bar extending toward midline; pigment less dark above anal photophores.

Distribution (Fig. 63). Taken in numbers off the Philippines and off the south China coast; reported from peninsular India, although these reports may represent *P. tridentifer*.

Polyipnus oluolus n. sp.

Figure 67

Holotype BCFH 2562; 11° 18'N, 162° 06'E; 12/9/56; R/V HUGH M. SMITH, cruise 37; Station 43.

Species distinction. Differs from *P. indicus* and *P. nuttingi* in its much broader body; post-temporal spine characteristics; triangular abdominal keel scales; supra-anal, supra-abdominal, and subcaudal

photophore characteristics; and posterior extension of dorsal fin rays to end of anal photophores.

Description. D. 14; A. 15; P. 13; total gill rakers 19; vertebrae 33.

Known only from holotype, 33 mm SL; body very broad, narrowing abruptly to short narrow caudal peduncle; body depth 1.3 times into SL; post-temporal spine length more than one-half diameter of orbit, extends to origin of dorsal spine, very spinose dorsally and laterally; frontal ridges almost vertical, spinose; postabdominal spines well developed; abdominal keel scales extend well beyond ventral body margin; these scales sharply triangulate, coming to a single or double point ventrally; subcaudal scales smooth; first supra-abdominal photophore raised considerably above other two; subcaudal photophores raised well above anals; first supra-anal photophore noticeably lower than second

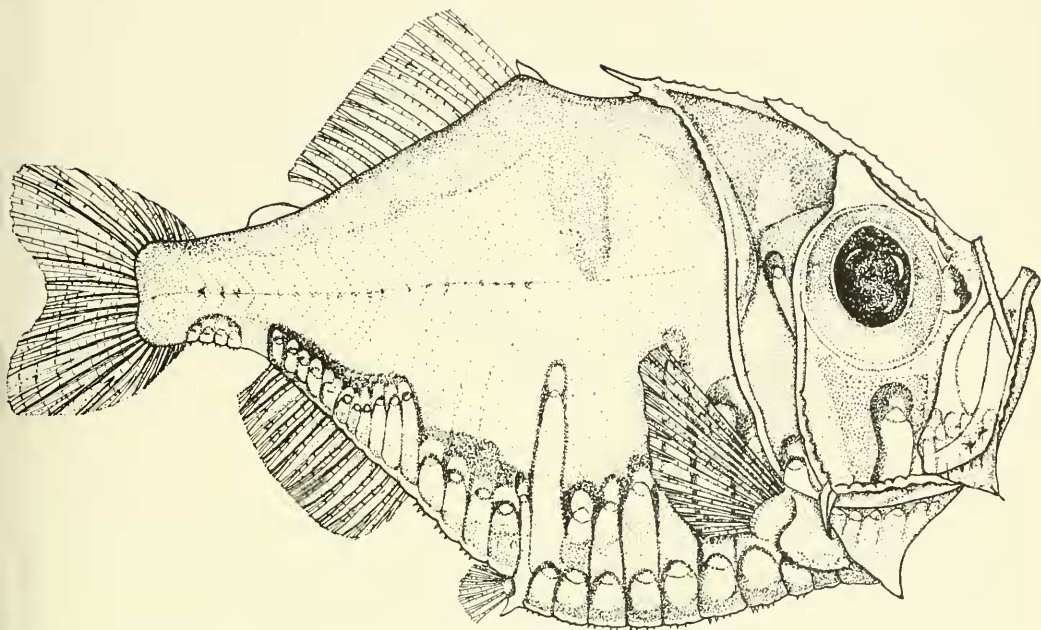


Figure 68. *Polyipnus indicus*; after Schultz, 1961.

which is lower than third; anal photophores in two distinct groups; jaws large; teeth small, several recurved ones in upper jaw; vomerine teeth well developed; gill rakers medium, spinose; in preservative pigment somewhat darker dorsally; pigment striations present on trunk.

Holotype: measurements (mm): SL 32.9, BD 25.7, JL 08.3, CP 03.9; meristics: GR 19, D 14, A 15, anal photophores 7; name: from the Hawaiian "oluolu," which means happy.

Distribution (Fig. 63). Known only from a single capture near the Marshall Islands.

Polyipnus indicus Schultz

Figure 68

Polyipnus indicus Schultz, 1961: 645 (holotype BMNH; off Zanzibar; not seen; paratype USNM 179897; seen); 1964: 241.

Polyipnus nuttingi: Norman, 1939: 20.

Species distinction. See *P. oluolus* (p. 90); differs from *P. nuttingi* by its longer, sharper post-temporal spines, less extended

abdominal keel scales, less spinose ventral border of lower jaw, photophore characteristics, presence of spiny subcaudal keel scales, generally lower gill raker number, and shorter post-temporal base-to-dorsal spine length compared to post-temporal spine length.

Description. D. 13–14; A. 15–16 (17); P. (12) 13–14; total gill rakers 20–21 (22); vertebrae 33–34.

Largest specimen less than 55 mm SL; trunk tapering to long caudal peduncle; post-temporal spine long, thin, its length greater than one-half the diameter of orbit; basal post-temporal spine short; preopercle spine long, curving anteriorly; frontal ridges minutely spinose; abdominal keel scales do not extend much below ventral body margin, these scales with multiple spines; subcaudal scales spinose; supra-abdominal photophores in steplike arrangement with first photophore raised substantially above second; supra-anal photophores not well separated from anals; jaws large; teeth minute; underside of

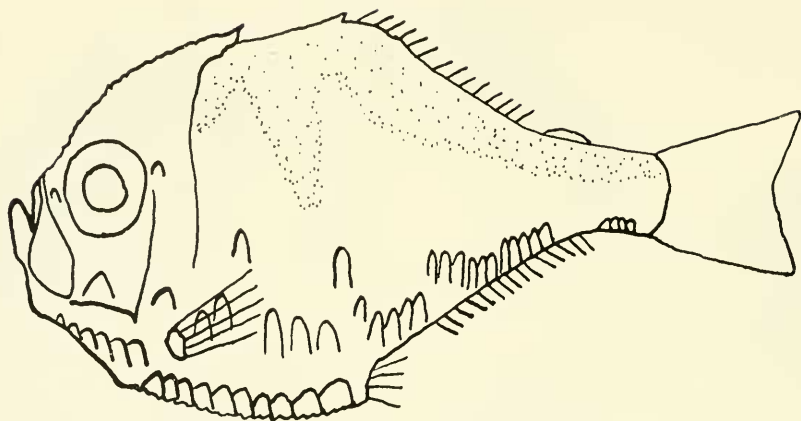


Figure 69. *Polyipnus nuttingi*; modified from Gilbert, 1905.

lower jaw smooth to slightly spinose; gill rakers short to medium with rough spinose internal surfaces; pigment in preservative dark dorsally and dark above anal photophores, dark pigment bar extends to midline; pigment in myomere-like striations on trunk, with definite pigment spots along posterior midline.

Distribution (Fig. 63). Known from three localities in the Indian Ocean along the east African coast from the equator to 30°S; reports of *P. spinosus* from this area may represent *P. indicus*.

Polyipnus nuttingi Gilbert

Figure 69

Polyipnus nuttingi Gilbert, 1905: 609 (holotype USNM 51599; Hawaii; seen); Fowler, 1949: 42; Haig, 1955: 321; Schultz, 1961: 640; 1964: 247.

Species distinction. See *P. oluolus* (p. 90) and *P. indicus* (p. 91).

Description. D. (12) 13–14; A. 15–16; P. 13–14; total gill rakers (21) 22–24; vertebrae 33–34.

Largest specimen less than 65 mm SL; body broad, tapering to long narrow caudal peduncle; post-temporal spine stout, relatively short (less than one-half eye diameter), slightly spinose dorsally; frontal ridges more vertically oriented than *P.*

indicus and minutely spinose; preopercle spine short, curving anteriorly; abdominal keel scales with multiple spines; these scales extend well below ventral body margin; post-temporal spine length less than one-half the distance from its base to point of dorsal blade; subcaudal scales smooth; supra-abdominal photophores arranged in a straight line, steplike arrangement; the three supra-anal photophores separated slightly but definitely from anal photophore group; jaws large; teeth minute; undersurface of lower jaw markedly spinose; gill rakers long, spinose on internal surface; dorsal spine high; pigment in preservative similar to *P. indicus*, although dorsal pigment bar is longer and broader.

Distribution (Fig. 63). Known only from the Hawaiian Islands where it appears to be an endemic.

Polyipnus laternatus Garman

Figure 70

Polyipnus laternatus Garman, 1899: 238 (holotype MCZ 27945; off Barbados; seen); Parr 1937: 49; Schultz, 1961: 639; 1964: 241.

Polyipnus spinosus: Brauer, 1906: 121 (in part) Goode and Bean, 1896: 127; Rivero, 1936: 56 (?).

Species distinction. Both *P. laternatus* and *P. omplus* differ from *P. aquavitus* and *P. unispinus* by their higher meristic

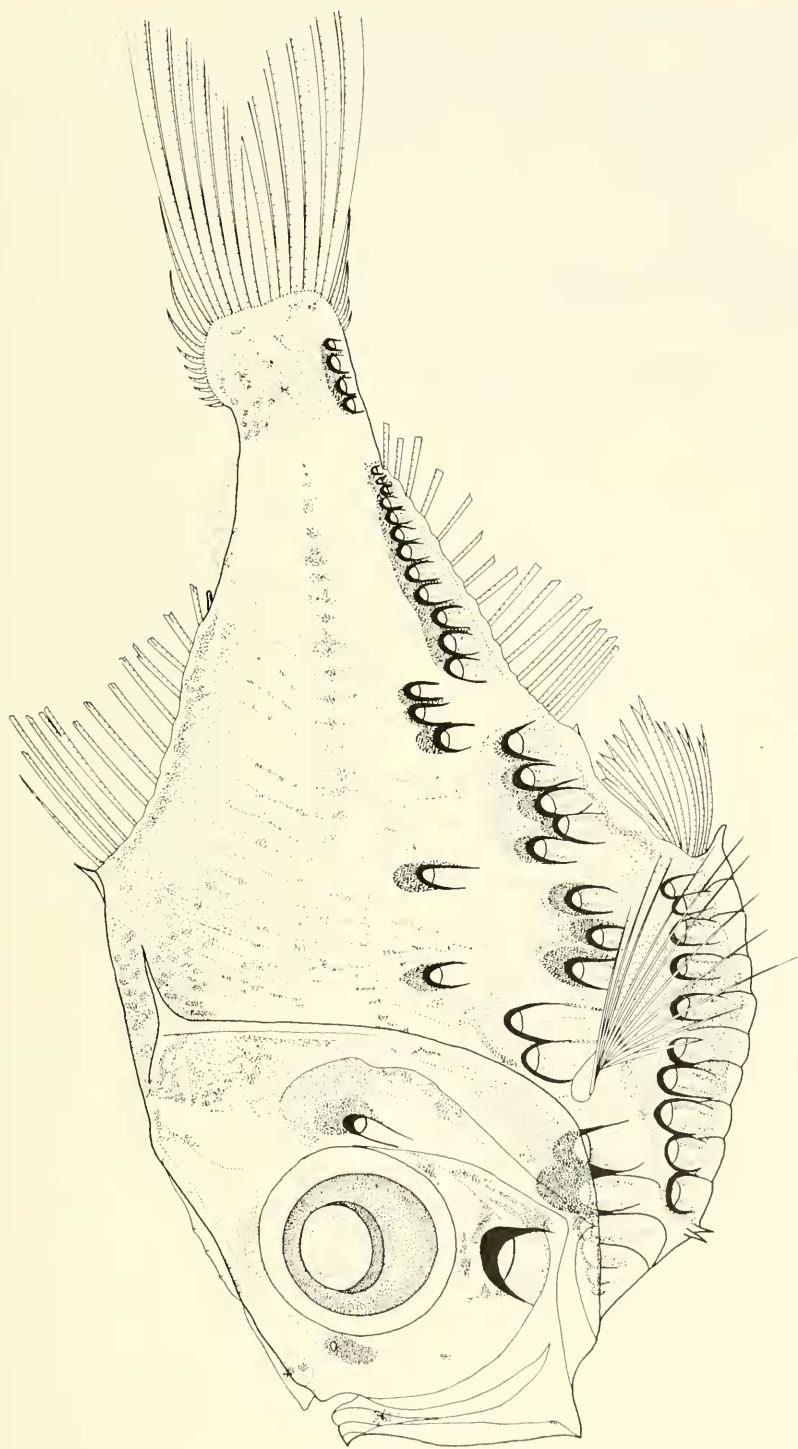


Figure 70. *Polyipnus lateratus*; R/V OREGON; Station 3609; SL 25 mm.

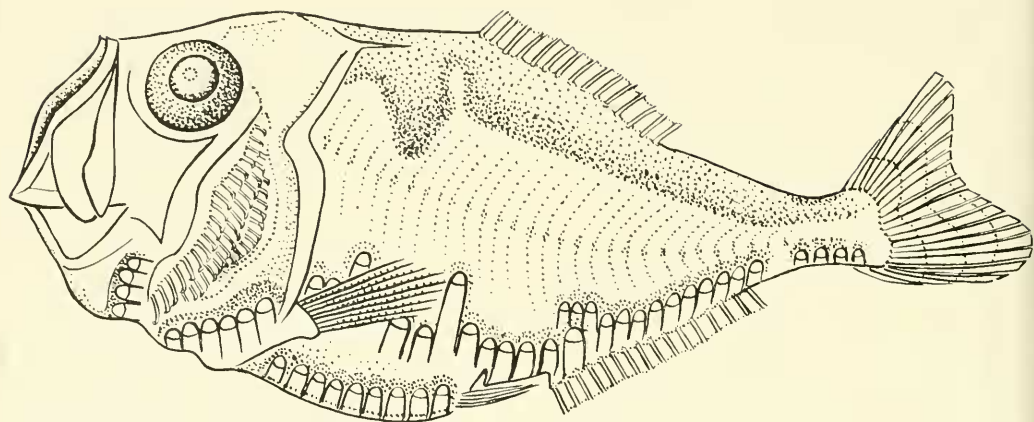


Figure 71. *Polyipnus omphus*; R/V DISCOVERY; Station 5509; SL 43 mm.

counts; shorter preopercle and dorsal spines; broader body, photophore and pigment characteristics. *P. laternatus* differs from *P. omphus* in its broader caudal peduncle; shorter, more compact subcaudal photophores, supra-anal and supra-abdominal photophore characteristics, slightly shorter preopercle spine, and relatively larger eye.

Description. D. 13–14 (15); A. (15) 16–17; P. 13–14; gill rakers (18) 19–22; vertebrae 32–33 (34).

Small to medium size species, rarely exceeding 55 mm SL; body relatively long and narrow, tapering into broad caudal peduncle, its width greater than width of subcaudal photophores; eye large, orbital diameter usually less than six times into SL; post-temporal spine long, thin, its total length variable (usually about one-half the diameter of orbit); dorsal spine short; preopercle spine short, broad, triangulate; abdominal keel scales smooth, not extended far beyond body margin; subcaudal photophores closely allied, little space between each photophore; supra-anal photophores raised well above anals, with first supra-anal slightly lower than second; first supra-abdominal photophore raised well above other two; second supra-abdominal even with or lower than third; jaws medium to small; teeth minute; vomerine

and palatine teeth small but prominent; gill rakers long, spinose on inner surface; pigment in preservative dark dorsally, dark pigment bar usually does not reach midline; prominent, dark spots along trunk midline; myomere-like pigment striations dorsally and vertically from midline.

Distribution (Fig. 63). Restricted to the western Atlantic; abundant in the Caribbean off Venezuela and the central American coast, in the lesser Antilles, off Puerto Rico, Cuba, and in the straits of Florida; not reported from the Gulf of Mexico or the east coast of North America.

Polyipnus omphus n. sp.

Figure 71

Holotype BMNH: 11° 21'S, 48° 58'E; 8/21/64. R/V DISCOVERY; Station 5509.

Polyipnus laternatus: Kobayashi, 1963: 179; Kottaus, 1967: 22 (otoliths, photo.).

Species distinction. See *P. laternatus* (p. 92). Both *P. laternatus* and *P. omphus* differ from *P. aquavitus* and *P. unispinus* by their higher meristic counts; shorter preopercle and dorsal spines; broader body, photophore and pigment characteristics. *P. laternatus* differs from *P. omphus* in its broader caudal peduncle; shorter, more compact subcaudal photophores; supra-anal and supra-abdominal photophore

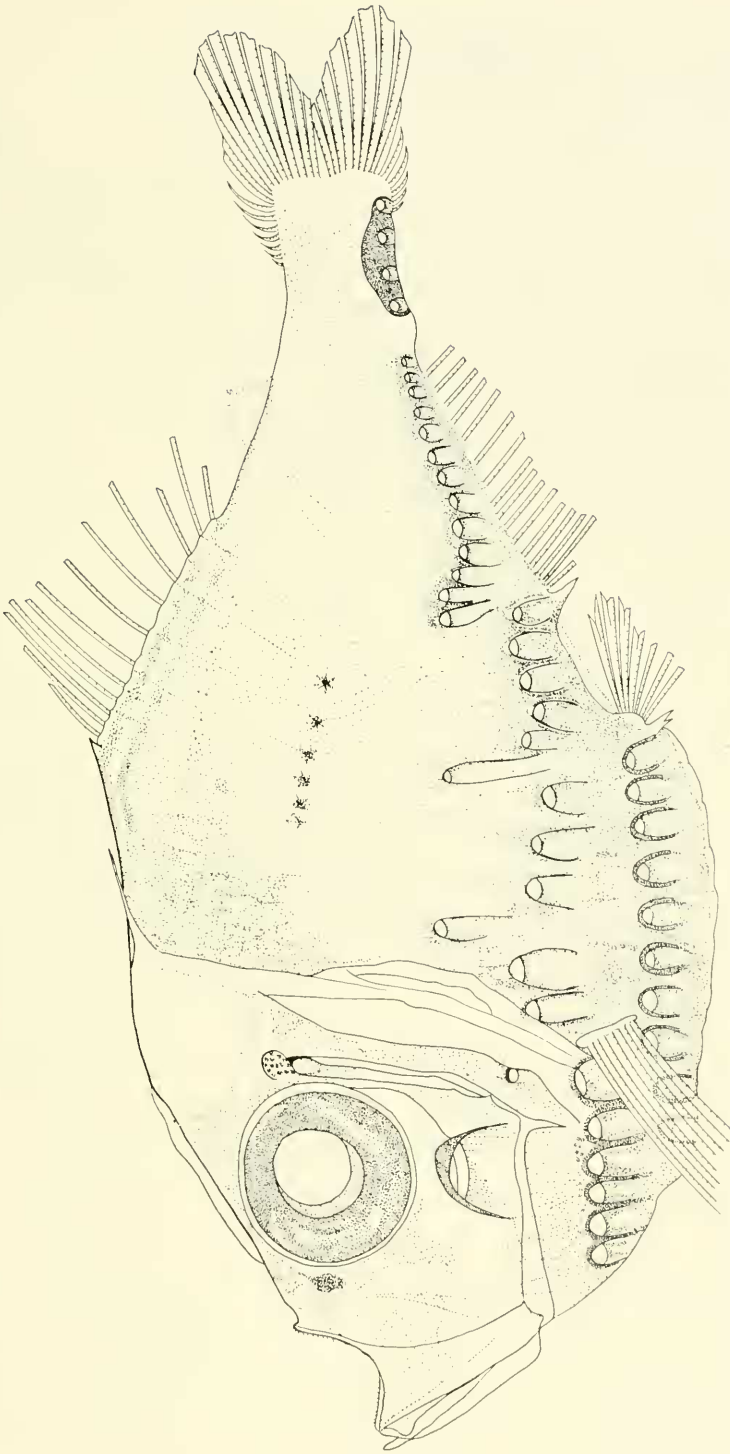


Figure 72. *Polyipnus aquavitus*; R/V GALATHEA; Station 551; SL 32 mm.

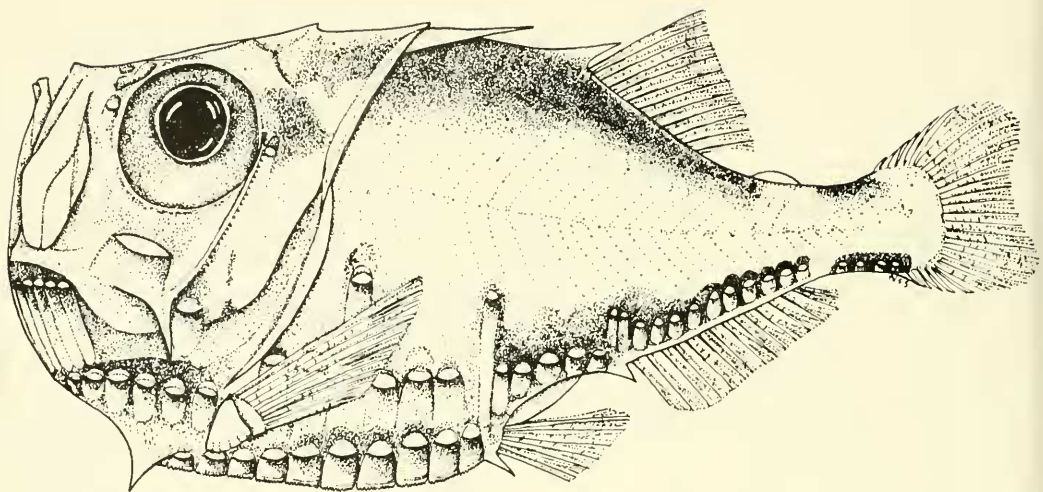


Figure 73. *Palyipnus unispinus*; after Schultz, 1938.

characteristics; slightly shorter preopercle spine; and relatively larger eye. The single specimen from the Pacific (SIO 60-236-101) appears slightly different phenotypically from the Indian Ocean forms. These two populations should be further examined when such material is available.

Description. D. 14-15; A. 16; P. 13-14; gill rakers 18-21; vertebrae (33).

Largest specimen less than 50 mm SL, body narrow, tapering into narrow caudal peduncle; its greatest depth less than length of subcaudal photophore group; eye relatively small, orbital diameter greater than six times into SL; post-temporal spine long, about one-half the diameter of orbit (or greater); dorsal spine short; preopercle spine short, narrowly triangulate; abdominal keel scales smooth, not extending far beyond body margins; subcaudal photophores spaced apart (about width of a photophore between them), distance between subcaudal and anal photophores about the same as length of one of the former; supra-anal raised only slightly above anals, with first supra-anal higher than second; supra-abdominal photophores in an oblique straight line; jaws medium; teeth minute; definite vomerine teeth present; gill rakers long, spinose; in pre-

servative, pigment dark dorsally with broad, dark bar reaching to or near midline; dark pigment spots along trunk midline with pigment striations radiating from them; dark pigment above ventral photophores.

Holotype: measurements (mm): SL 40.1, BD 20.0, JL 06.1, CP 03.4; meristics: GR 19, D 14, A 16; anal photophores 11; name: from the Marathi word "omphus," roughly translated as "unwanted."

Distribution (Fig. 63). Extremely disjunct range; known from a few specimens north of Madagascar in the Indian Ocean and from a single capture in the Central Pacific north of the Marquesas Islands. Additional record: 00°00', 165°42.5'W.

Polyipnus aquavitus n. sp.

Figure 72

Holotype ZMUC P20969; 33° 42'S, 151° 51'E 11/13/51; R/V GALATHEA; Station 551.

Species distinction. See *P. laternatus* (p. 92). *P. unispinus* differs from *P. aquavitus* by its longer dorsal and preopercle spines, spinose preopercle and ventral keel plates, shorter subcaudal to anal photophore distance, longer postabdominal and

anal pterygiophore spines, and its narrower trunk and caudal peduncle.

Description. D. (11) 12–13; A. 15–16; P. (12) 13–14; gill rakers 12–14; vertebrae (35).

Largest specimen less than 45 mm SL; body narrow, tapering into narrow caudal peduncle; its least depth less than length of subcaudal photophores; post-temporal spine long, length greater than one-half the diameter of orbit; dorsal spine short; preopercle spine short, sharp, length less than one-half the diameter of orbit; second preopercle spine reduced; lateral surface of preopercle smooth; abdominal keel scales smooth, not extended ventrally; supra-anal photophores only slightly raised from anals; first supra-anal photophore raised above second and third; anal-subcaudal photophore distance one-fourth or greater than length of latter; mouth small; teeth minute; gill rakers short to medium; in preservative, body pigment is dark over abdomen and trunk; pigment often present in band at base of caudal rays, few dark pigment spots along lateral midline.

Holotype: measurements (mm): SL 38.5, BD 17.7, JL 07.0, CP 03.6; meristics: GR 13, D 13, A 15, anal photophores 10; name: from the Danish national drink, akvavit.

Distribution (Fig. 63). Taken abundantly off Sidney, Australia, and known from single captures in the Banda Sea and between Tasmania and New Zealand.

Polyipnus unispinus Schultz

Figure 73

Polyipnus unispinus Schultz, 1938: 137 (holotype USNM 103153; Philippines; seen); 1961: 643; 1964: 247.

Species distinction. See *P. laternatus* (p. 92). Differs from *P. aquavitus* by its longer dorsal and preopercle spines, spinose preopercle and ventral keel scales, shorter subcaudal to anal photophore distance, longer postabdominal and anal pterygiophore spines, and its narrower trunk and caudal peduncle.

Description. D. 12–13 (14); A. 13–15; P. 12–13; gill rakers (11) 12–14; vertebrae (35–36).

Small, possibly a “dwarf” species, none yet exceeding 40 mm SL; body narrow, tapering into long narrow trunk and caudal peduncle; post-temporal spine long, almost equal to orbital diameter; dorsal spine long, high; its length about equal to one-half of orbital diameter; preopercle spine long, greater than one-half of orbital diameter; a well-developed second preopercle spine usually present; dorsal lateral surface of preopercle spinose; abdominal keel scales spinose ventrally; postabdominal and anal pterygiophore spines well developed; supra-anal photophores almost continuous with anals; first two supra-anals raised markedly above third; distance between subcaudal and anal photophores less or equal to one-fourth the length of the latter; mouth small; teeth minute; vomerine teeth prominent; gill rakers short to medium, well spaced; in preservative pigment slightly darker dorsally; abdomen and trunk relatively dark.

Distribution (Fig. 63). Taken in small numbers off the Philippines, and represented by two small samples from the Banda Sea.

Polyipnus triphanos Schultz

Figure 74

Polyipnus triphanos Schultz, 1938: 140 (holotype USNM 103027; Pescador Islands; seen); 1961: 640; 1964: 247.

Species distinction. See *P. asteroides* (p. 99); differs from *P. polli* by its higher anal photophore number, lower gill raker and dorsal ray counts, a straight ventral anal photophore margin, and the raised dorsal pigment border above the supra-anal photophores.

Description. D. 11–12; A. 17 (18, 19); P. 13–14; gill rakers (15) 16–18 (19); vertebrae (33).

Body broad, tapering into narrow caudal peduncle; its height slightly greater than length of subcaudal photophore group;

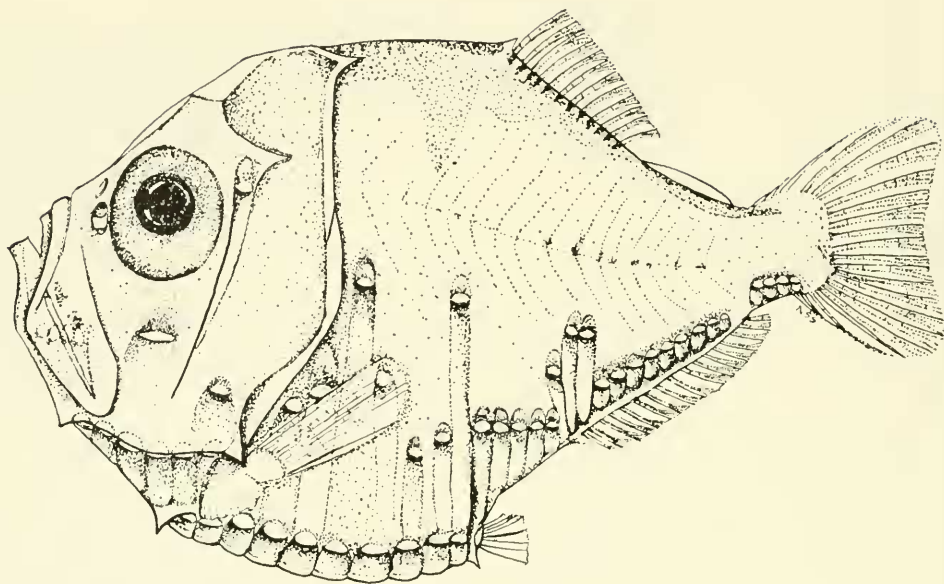


Figure 74. *Polyipnus triphanos*; after Schultz, 1938.

post-temporal spine short, needlelike; dorsal spine short; preopercle spine short, triangulate; abdominal keel scales extend only slightly below ventral body margin; first supra-anal photophore markedly lower than other two; first supra-abdominal raised above others, second lower than third, jaw medium to small; teeth minute; gill rakers medium, spinose; in preservative, pigment dark dorsally; dark pigment bar reaches almost to midline followed by light stripe reaching towards mid-dorsal line; ventral margin of dark dorsal pigment markedly raised on trunk above supra-anal photophores; pigment spots present on trunk midline, striations not distinct.

Distribution (Fig. 63). Known only from a few captures off the Philippines. Additional Record: 05° 01.0'S, 127° 57'E.

Polyipnus polli Schultz

Figure 75

Polyipnus polli Schultz 1961: 635 (holotype MRAC 95092; south east Atlantic; not seen, paratype USNM 179878; seen); 1964: 247; Blache, 1964: 71; Backus et al., 1965: 139.

Polyipnus lateruatus: Norman, 1930: 305; Fowler 1936: 1208; Poll, 1953: 65.

Polyipnus spinosus: Smith, 1953: 102 (?).

Species distinction. See *P. asteroides* (p. 99) and *P. triphanos* (p. 97).

Description. D. 14–15 (16); A. (15) 16–17; P. 13–14; gill rakers (20) 21–23; vertebrae 32–33.

Medium to small species, seldom exceeds 50 mm SL; body and trunk broad, narrowing abruptly to small, short caudal peduncle; post-temporal spines short, needlelike; dorsal spine short; preopercle spine short, triangulate; abdominal keel scales smooth; not extended ventrally; first supra-anal photophore lower than other two; first supra-abdominal raised well above second which is approximately even with third; subcaudal photophore group short, about equal to width of dorsal pigment bar at its center; body margin below anal photophores markedly curved; anal pterygiophores extend well beyond body margin; jaws small; teeth minute; gill rakers medium to long, and spinose; in preservative, pigment dark dorsally with pigment

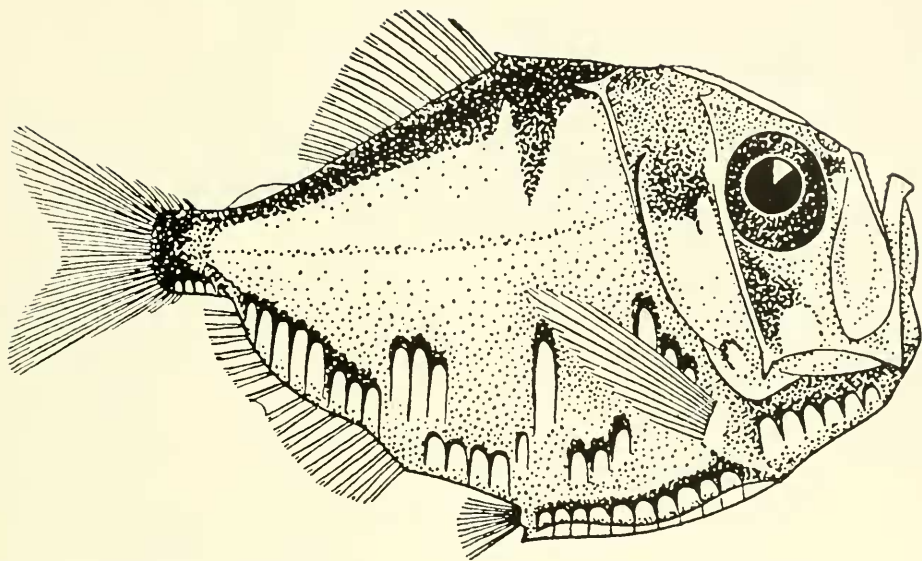


Figure 75. *Polyipnus polli*; after Norman, 1930.

bar reaching toward midline; ventral border of dorsal pigment in straight line, from lateral photophore to caudal peduncle; dark pigment spots on midline and between midline and border of darker dorsal pigment; pigment striations present on trunk.

Distribution (Fig. 63). Restricted to the southeastern Atlantic along the west African coast from the Gulf of Guinea to 10°S latitude.

Polyipnus asteroides Schultz

Figure 76

Polyipnus asteroides Schultz, 1938: 138 (holotype USNM; West Indies; not seen); 1961: 640; 1964: 247; Scott, 1965: 1303.

Polyipnus lateruatus: Jespersen, 1934: 15.

Species distinction. *P. asteroides*, *P. triphanos*, and *P. polli* differ from *P. meteor*, *P. matsubara*, *P. kinciensis*, and *P. ruggeri* by their lack of teeth on the posterior vomerine shaft, and by supra-abdominal and supra-anal photophore characteristics; *P. asteroides* differs from *P. polli* by its greater number of anal photophores, less

broad trunk, longer subcaudal photophore group, relatively straight anal photophore margin, and attainment of greater size; differs from *P. triphanos* by its less broad body, higher gill raker and dorsal ray counts, and body pigment characteristics.

Description. D. 14–16 (17); A. (15) 16–17 (18); P. (12) 13–14 (15); gill rakers 20–23 (24); vertebrae 32–33.

Large to giant species, often exceeds 70 mm SL; body relatively broad, tapering evenly to narrow but short caudal peduncle, its greatest depth greater than length of subcaudal photophores; post-temporal and dorsal spines short (less than one-fourth eye diameter); preopercle spine very short, triangulate; abdominal keel scales extend slightly below ventral body margin; first supra-anal photophore markedly lower than second; first supra-abdominal photophore raised well above other two, second and third supra-abdominals usually about same height; jaws medium to large; teeth minute; gill rakers medium to long, spinose on internal surface; in preservative, pigment dark dorsally; dark pigment bar extends toward but never

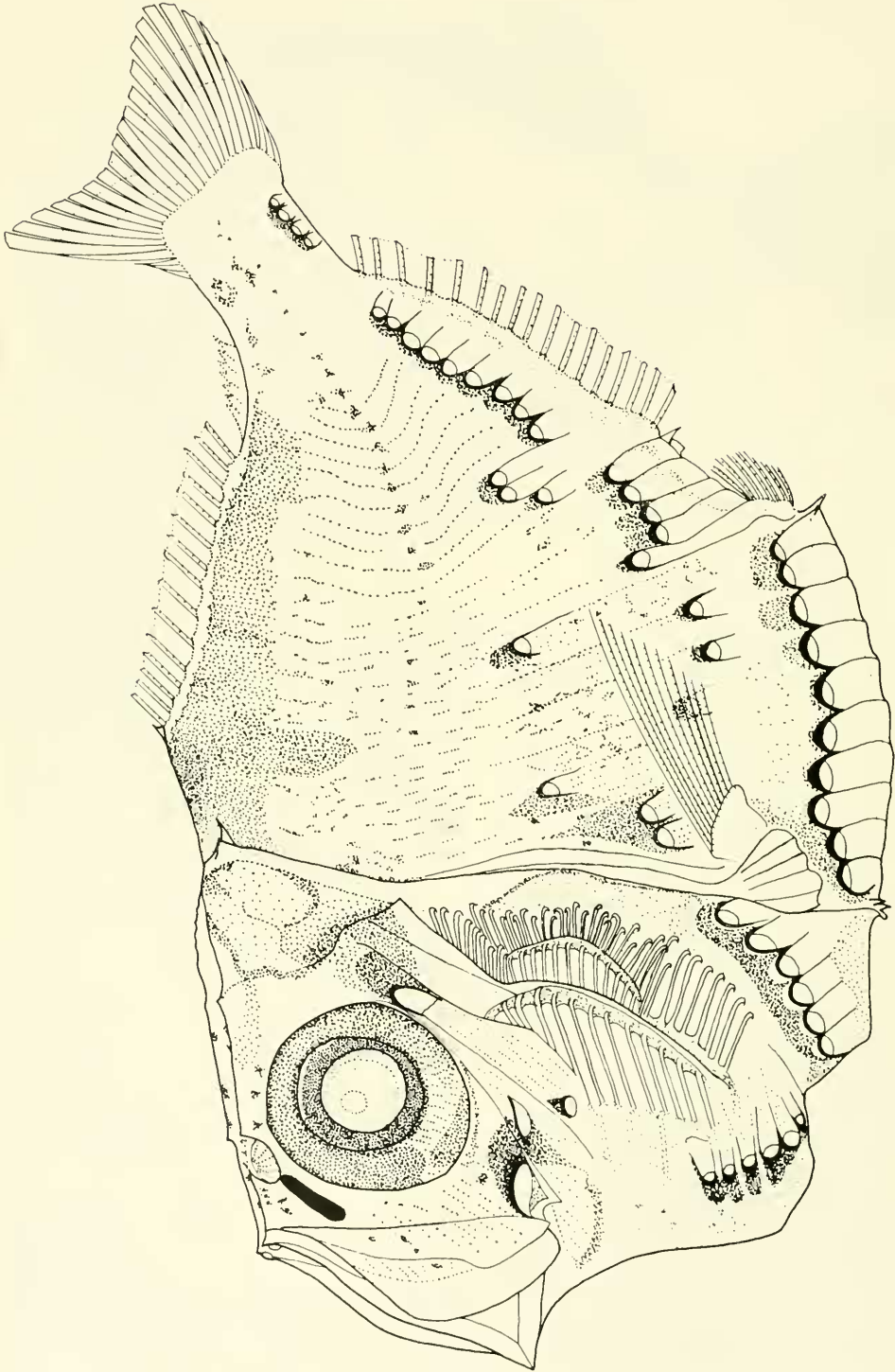


Figure 76. *Polyipnus asteroides*; R/V CHAIN, Cruise 60; Station 1295; SL 38 mm.

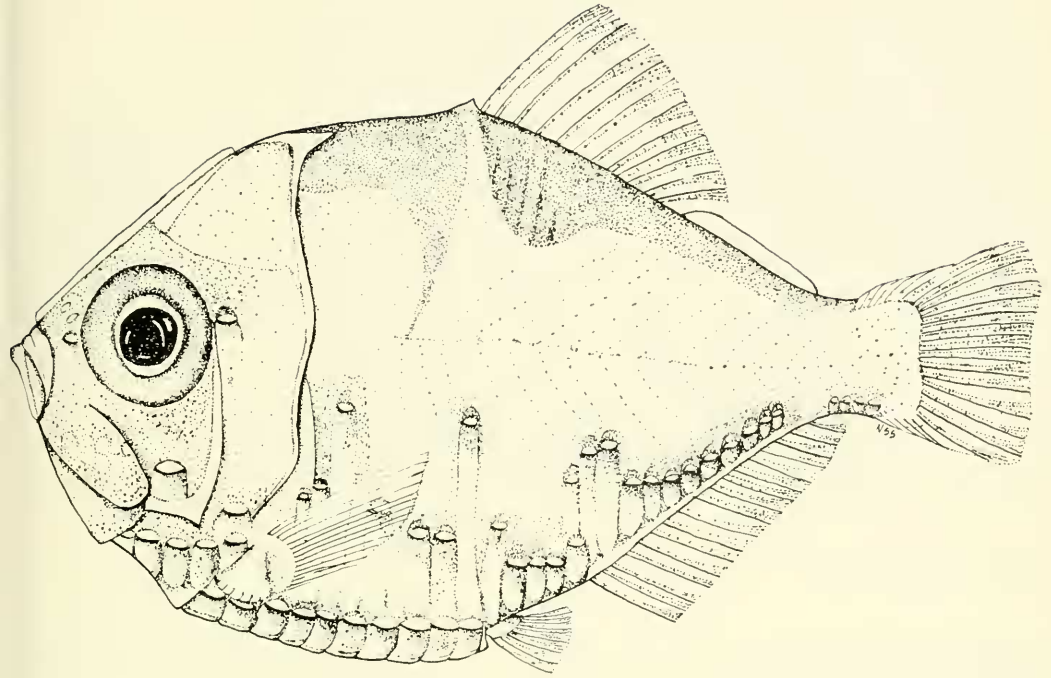


Figure 77. *Polyipnus matsubarai*; after Schultz, 1961.

reaches midline; lateral border of dark dorsal pigment straight from dorsal spine to caudal peduncle; dark pigment spots mark lateral midline, pigment striations present on trunk.

Distribution (Fig. 63). Restricted to the western North Atlantic; abundant in the Caribbean and Gulf of Mexico from the coast of Venezuela to the straits of Florida; occurs off the outer islands of the West Indies and less abundantly along the east coast of North America; a single capture has been reported as far north as the Gulf of Maine.

***Polyipnus matsubarai* Schultz**
Figure 77

Polyipnus matsubarai Schultz, 1961: 641 (holotype USNM 179793; Kumanonada, Japan; seen); 1964: 247.

Polyipnus japonicus Schultz, 1961: 643; 1964: 247.

Polyipnus asteroides: Matsubara, 1941: 2; 1950: 192.

Species distinction. See *P. asteroides* (p. 99); differs from *P. ruggeri*, *P. kiwiensis*, and *P. meteori* by its higher gill raker count, long narrow caudal peduncle, and very narrow dorsal pigment bar.

Description. D. 12 (13); A. 16-17; P. (12) (13) 14-16; gill rakers 22-24; vertebrae 33.

Largest specimens have not exceeded 50 mm SL; body broad, tapering into long, relatively narrow caudal peduncle; its length equal to or greater than its greatest depth; post-temporal spine rather long and needlelike, its length about one-fourth the orbital diameter; dorsal spine short; preopercle spine short, triangulate; abdominal keel scales smooth, with no ventral extension; first supra-abdominal photophore raised above second which is equal to or slightly raised above third; supra-anal photophores in steplike arrangement, the third being highest; first three anal photophores even and parallel to midline; jaws

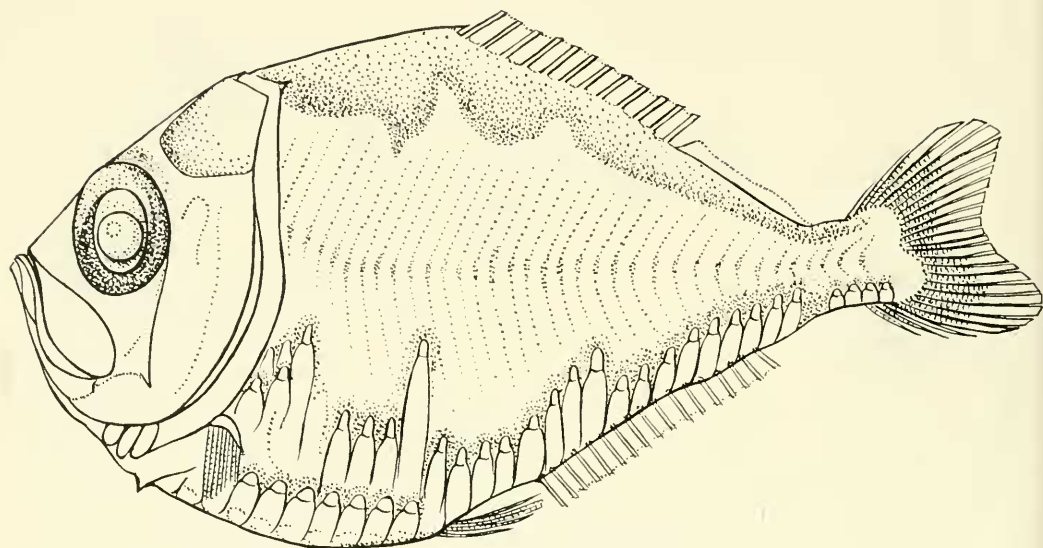


Figure 78. *Polyipnus ruggeri*; R/V TUI; New Zealand; SL 47 mm.

medium; teeth present on long posterior shaft of vomer lying ventral to parasphenoid, resulting in three distinct tooth bearing areas on the vomer; gill rakers medium; in preservative, dorsal pigment bar is extremely narrow and reaches to midline; dorsal pigment border is broken by light stripe behind pigment bar, reaching broadly to mid-dorsal line; dorsal pigment border raised slightly above supra-anal photophores; small, dark pigment spots mark lateral midline.

Distribution (Fig. 63). Abundant in the waters off Japan in the North Pacific; a single capture in the mid-North Pacific represents this species.

Polyipnus ruggeri n. sp.

Figure 78

Holotype DMNZ 4670; 31° 57'S, 177° 38'E; 7/24/62; R/V TUI.

Species distinction. Differs from the *P. asteroides* (p. 99) group by dentition and photophore characteristics and from *P. matsubarae* (p. 101) by dorsal pigment and gill raker characteristics; differs from *P. meteori* and *P. kiwiensis* by its dorsal pig-

ment characteristics, higher gill raker count, and photophore patterns; further differs from *P. kiwiensis* by its smaller, rounder eye, longer, narrower caudal peduncle, and lesser distance between frontal crests (interorbital).

Description. D. 12; A. 16-17; P. 15; gill rakers 18; vertebrae (33).

Largest specimen less than 60 mm SL; body broad, tapering into somewhat long and narrow caudal peduncle; its length greater than depth; post-temporal spine short, rough surfaced dorsally, less than one-fourth of the diameter of orbit; dorsal spine short, low; preopercle spine triangular; eye large, round, its length about equal to width; greatest distance between frontal crests (interorbital) less than or equal to length of subcaudal photophore group; abdominal keel scales not extended ventrally; supra-abdominal photophores in essentially straight line, first may be slightly raised above third; first supra-anal photophore noticeably lower than second, which is lower than third; jaws medium to large; teeth present on posterior vomerine shaft; gill rakers medium, slightly spinose; in preservative, pigment dark dorsally with a

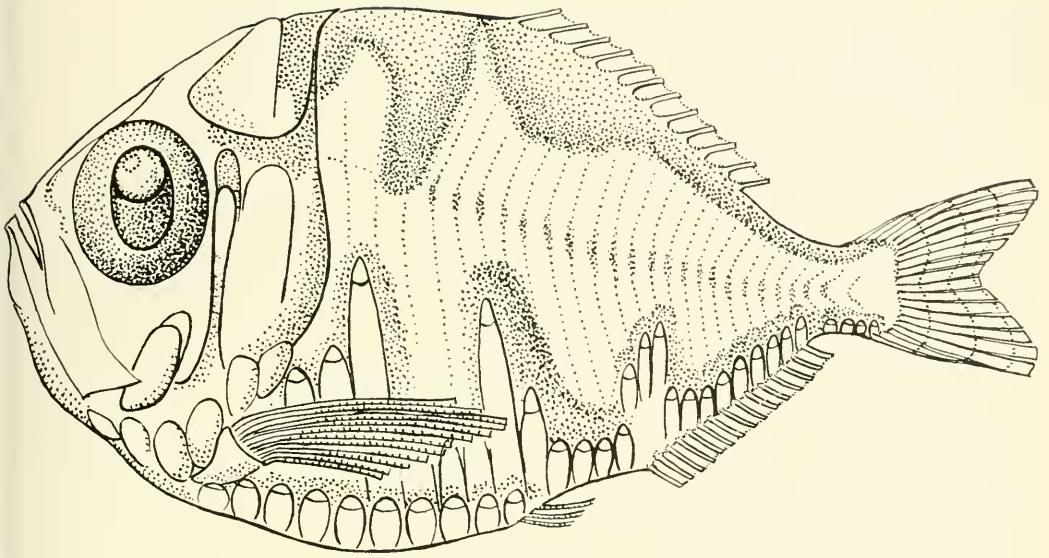


Figure 79. *Polyipnus kiwiensis*; R/V TUI; New Zealand; SL 60 mm.

very reduced pigment bar; much reduced light stripe behind bar does not reach mid-dorsal line; ventral border of dorsal pigment raised above supra-anal photophores; small dark pigment spots present on lateral midline.

Holotype: measurements (mm): SL 46.8, BD 30.3, JL 09.7, CP 05.5; meristics: GR 18, D 12, A 17; anal photophores 9; name: named in honor of New Zealand's national sport, rugby.

Distribution (Fig. 63). Known only from a few small captures off Wellington, New Zealand, and west of the Kermadec Islands.

Polyipnus kiwiensis n. sp.

Figure 79

Holotype DMNZ 4802; 36° 50'S, 176° 10'E; 9/26/62; R/V TUI.

Species distinction. Differs from *P. asteroides* (p. 99) group by photophore characteristics and teeth on posterior vomerine shaft; from *P. matsubarai* by gill raker number and dorsal pigment characteristics (*P. matsubarai*, p. 101); from *P. ruggeri* (p. 102) by dorsal pigment characteristics, eye size, gill raker number,

caudal peduncle, and interorbital crests; differs from *P. meteori* by its higher gill raker counts, larger eye and mouth, photophore and dorsal pigment characteristics.

Description. D. (11) 12; A. 16–17; P. 15–16; gill rakers 16–17; vertebrae (32) 33 (34).

Largest specimens less than 70 mm SL; body broad, tapering rather abruptly into short caudal peduncle; its depth about equal to its length; post-temporal spine short, less than one-fourth the diameter of orbit; dorsal spine short, preopercle spine triangulate; eyes extremely large, their diameter less than seven times into SL; greatest distance between frontal crests (interorbital), greater than length of sub-caudal photophore group; abdominal keel scales not extended ventrally; first and third supra-abdominal photophores about even and raised well above second; first supra-anal photophore noticeably lower than second, which is slightly lower than third; jaws large, broad; teeth well developed on posterior vomerine shaft and lower jaw; gill rakers medium; in preservative broad, dark, dorsal bar reaches to midline; light stripe posterior to dorsal

bar not reaching to mid-dorsal line; ventral border of dark dorsal pigment only slightly raised above supra-anal photophores; small dark pigment spots on lateral midline.

Holotype: measurements (mm): SL 59.5, BD 36.4, JL 14.3, CP 09.7; meristics: GR 17, D. 12, A. 17; anal photophores 10; name: from Kiwi—a New Zealand bird; in the vernacular, a Kiwi is a native of New Zealand.

Distribution (Fig. 63). Taken in moderate numbers near Red Mercury Island off the northeastern coast of North Island, New Zealand.

Polyipnus meteori Kotthaus

Polyipnus meteori Kotthaus, 1967: 27 (holotype IOES 20; off Seychelles, Indian Ocean; not seen).

Species distinction. See *P. asteroides* (p. 99), *P. matsubarae* (p. 101), *P. ruggeri* (p. 101), and *P. kiwiensis* (p. 103).

Description. (From description of holotype (Kotthaus, 1967) and photograph.) D. 12; A. 16; P. 15; gill raker number 13–15.

Known only from holotype (SL 37 mm); body broad, tapering to relatively long caudal peduncle (appears shorter than *P. matsubarae*); post-temporal spine needle-like, about equal to one-fourth the eye diameter; dorsal spine short; abdominal keel scales smooth, not extended ventrally; first and third supra-abdominal photophores about even and raised above second; first supra-anal markedly lower than second, which is lower than third; jaws medium; in preservative broad, dark, dorsal bar reaches to midline followed by light stripe which reaches mid-dorsal line; ventral border of dorsal pigment raised considerably above supra-anal photophores; dark pigment spots present on midline.

Distribution (Fig. 63). Known only from a specimen taken near the Seychelle Islands in the Indian Ocean; two juvenile *Polyipnus* from the east coast of Africa

may represent this species. Note: Key characters checked with holotype through the courtesy of Dr. Verner Larsen, ZMUC.

DISCUSSION AND CONCLUSIONS

Patterns of Distribution

The ecological distinctness of the family and the basic structural modifications involved in the peculiar body form were discussed above. Given this basic structural similarity, the respective genera have diverged morphologically and ecologically. This is apparent in the distinctive distribution pattern of each genus and is indicative of the types of distributions to be found in deep-sea fishes.

Polyipnus. Although *Polyipnus* has the basic adaptive attributes of a midwater fish, the genus—with the exception of isolated expatriates—is associated with land areas. Land-oriented distributions have been reported in midwater fishes (Ebeling, 1962; Nafpaktitis, 1968), but these have involved members of essentially pelagic genera. *Polyipnus* is a moderately speciose genus which has adapted solely to land associated environments. While continental slope areas are important, this genus occurs abundantly near oceanic islands well away from continental margins. Depth data are generally sparse, but indicate that *Polyipnus* is found from 50 m to 400 m. The extent of diurnal migration is unknown, although certain species have been reported near the surface at night off Japan (Haneda, 1952). The “pseudo-pelagic” environment of this species has not been extensively sampled in most areas. Species ranges are therefore incomplete, and little is known about population structure and vertical distribution. New species can be expected and additional revision will be required as collecting proceeds.

The peculiar distribution of this genus may be related to land-oriented food chains. There is an extensive amount of literature on the increased productivity associated with land areas and on the

occurrence of neritic forms of zooplankton. *Polyipnus* has specialized feeding habits, and two peculiar morphological features may be involved in its adaptation to a specialized niche. These features are the jaw and branchial morphology, and the enlargement of the otic region. An additional indication of biological differences from the other genera is the small number of juveniles collected with the adults. Much remains to be known about the biology and ecology of this genus, as well as its "pseudopelagic" environment.

Comparison of the essentially tropical and-oriented distribution of *Polyipnus* with other tropical shore species provides some interesting parallels. Tropical reef and shelf fish are diverse in the Indo-west Pacific region, with the Indo-Malayan area the most speciose (e.g., Ekman, 1967: 17). The number of species declines as one proceeds from this area. While present in many of the islands of outer Polynesia (Hawaii, Marquesas, Tuamotu archipelago), few shore species reach the western coast of the Americas. This is attributed to the wide stretch of open water in the eastern Pacific (the zoogeographic east Pacific barrier). Contributions of Indo-west Pacific elements to the tropical Atlantic are reduced by a similar, although not as restrictive, central Atlantic barrier, in addition to the African continent (Briggs, 1960, 1961). The tropical shore fauna is further characterized by its "modernness." It consists primarily of the most advanced and latest evolved fishes, with relicts and more primitive groups less well represented. Geographic endemics are common, especially near the more isolated island groups.

The largest number of *Polyipnus* species have been collected around the Philippine Islands. Eight of 17 known species occur in the tropical west Pacific. Endemics occur in New Zealand, Hawaii, and the Marshall Islands at the limits of the range in the Pacific. Three other species occur in the western Indian Ocean, thus accounting for 14 of 17 species in the Indo-west

Pacific. No species are reported from the eastern Pacific. The *P. spinosus* species complex is not found in the Atlantic; only three species occur there. Two are restricted to tropical and temperate America, and one to the west African coast. There are no trans-Panamanian species. Speciation tends to be geographic and endemics are numerous. Extensive sympatry between species complexes is rare. Life history features apparently restrict species to land-associated waters. No open-water pelagic populations are known, and barriers to gene flow among discontinuous populations appear considerable.

Here, then, is a classic tropical shore distribution in what appears to be the most primitive genus of the family (Ebeling, 1962, indicates some of the same features in *Melamphaes*). Since such a distribution is characteristic of lately evolved groups, it is interesting to speculate on the possible recent origin of *Polyipnus*. While primitive maurolicid gonostomatids are identified from the early Tertiary, *Polyipnus* as presently defined, is not. (It is not present in Tertiary Tethys or California deposits.) *Argyropelecus* is known from the Oligocene. Its distribution is worldwide (including the Tethys fauna), as are a number of gonostomatids (admittedly a different ecology and distribution pattern). *Polyipnus*, while primitive in axial skeleton characteristics, is nevertheless highly specialized in the cranial region. These characters may be the major adaptive features allowing *Polyipnus* access to its specialized niche, resulting in a new adaptive type which possibly arose relatively recently.

Argyropelecus. *Argyropelecus* species are characterized by broad worldwide high seas distributions. The genus is found in all tropical and temperate oceans, and is absent from polar seas. The limits of distribution are bounded approximately by the 5° isotherm at 200 m. Within these broad limits, however, distribution can be quite restricted with the result that worldwide species are broken up into a series of

disjunct populations which appear more or less isolated from each other.

In general, species occur vertically over the same depth range wherever they are found. With the exception of *A. gigas*, *Argyrolepecus* species are partial or incomplete diurnal migrators. At night many species ascend to above 300 m, often to about 200 m from their daytime depths of 400–500 m. Catches in the upper 100 m seldom involve large numbers of individuals. *A. aculeatus* is most distinct in its vertical migration, while *A. gigas*, the deepest living species, migrates very little. Within these broad limits (150–600 m) depth variability is high, indicating considerable microcomplexity (Appendix B). From bathyscaphe observations during the day, Perès (1958) reports *A. hemigymnus* from 250–600 m, with large concentrations from 400–500 m. Perès' and other bathyscaphe observations (Drs. R. Rosenblatt, R. Haedrich, and R. Richards, personal conversations) indicate that *Argyrolepecus* species do not school in the classical sense, but are somewhat isolated from one another. Catch data (Table 23) show the wide range in size distribution with large catches, another indication of nonschooling behavior.

Unlike many midwater fishes, the larvae and juveniles of *Argyrolepecus* are found in the adult environment (Table 23) (Ahlsrom, 1959). Over the range of a species distribution some gravid females and young juveniles were usually found. Large scale expatriation does not appear to be important. Wherever a species is found in an area in numbers it seems to represent a breeding population.

Argyrolepecus is represented by seven species in three species complexes. Species are morphologically distinct in most cases and, as with *Polyipmus*, broad sympatry within complexes is uncommon. Sympatry is limited to zones of mixing between allopatric species ranges when it occurs within species complexes. Dwarf and giant species occur. The giant species (*A. gigas*) is quite restricted in distribution, limited

essentially to zones of water-mass boundaries. The dwarf species (*A. hemigymnus*), while occurring in the relatively unproductive central water masses, is abundant in highly productive temperate and eastern boundary current waters.

Sternoptyx. *Sternoptyx* species have broad worldwide pelagic distributions similar to *Argyrolepecus* and with approximately the same geographic limits. The juveniles are found in the adult environment, although larger individuals may be found slightly deeper. There is no indication of expatriation. *Sternoptyx* is less speciose than *Argyrolepecus* and species distinctions are much less marked. Two of the three species (*S. diaphana* and *S. obscura*) have wide allopatric ranges, with restricted areas of overlap. *S. pseudobscura* and *S. diaphana* are broadly sympatric over much of their respective ranges.

Vertically, all species are deep living (500–1500 m) and show little diurnal migration. Variability in catch size ranges indicates that *Sternoptyx* probably does not school.

Geographic Variation

Mayr (1963: 333) makes the following points in a discussion of geographic variation: Every population of a species differs from all other populations genetically, and when sufficiently sensitive tests are employed, also biometrically. The degree of divergence between different populations of a species ranges from near complete identity to distinctness almost of species level. Various characters of a species may and usually do differ independently. The characters of a given population have at least a partial genetic basis, and in most cases tend to remain rather constant through the years.

The absence of detectable differences between horizontally disjunct populations is not necessarily indicative of no population differences. In the present study, methods were not particularly sensitive, nor were many characters used. However,

where differences do exist one can delimit populations which, when coupled with distributional data, should add to our understanding of the environmental and biological factors which are important in restricting species distributions.

Most of the patterns of geographic variation outlined by Mayr are present in *Argyrolepecus* and *Sternoptyx*. *A. gigas*, which appears to have the most disjunct distribution, displayed no detectable differences between widely separated populations. Characters which are constant in one species, vary in another. In general, however, population differences were found between geographically isolated populations as indicated by horizontal distributions. The statistical characteristics of a population of at least one species (*A. aculeatus*) remained constant over a period of two years. Population limits can be quite broad, and usually population boundaries are correlated with species boundaries in the same area. However, where species' ranges cross major zoogeographic boundaries, populations on either side of this boundary may be quite distinct (e.g., *A. hemigymnus* in the North Atlantic).

Population boundaries and morphological diversification are more obvious in the shallow-dwelling *Argyrolepecus* than in the deeper-living and nonmigrating *Sternoptyx* (Ebeling and Weed, 1963, noted this for *Melamphaes* and *Scopelogadus*). Distributions of deeper living pelagic invertebrates also show this pattern (David, 1963; Grice and Hulsemann, 1967) which is apparently correlated with the decrease in environmental differences with depth between different areas of the oceans. Additional study is necessary to fully appreciate and delimit the population structure of both genera.

Distributional Factors

A considerable amount of literature is now available emphasizing the importance of water masses in the distribution of deep-sea organisms (Bieri, 1959; Ebeling, 1962;

Johnson and Brinton, 1963, among others). Discussions of water masses—their formation, location, and identification—are numerous (e.g., Sverdrup et al., 1960; Ebeling, 1962), and each year knowledge of the extent, boundaries, and origin of discontinuities in the oceans increases. Table 24 relates the distribution of the species of *Argyrolepecus* and *Sternoptyx* to the various water masses as presently defined. Several interesting conclusions result. One species (*A. aculeatus*) is limited to central water masses within the great gyre systems of the central oceans. Two species (*A. lychnus*, *S. obscura*) are limited to the east Pacific equatorial water mass and the transitional waters at its boundary. As presently defined, water masses are too broad to accurately describe many distributions; this is particularly so in the Atlantic. While the label "central" or "equatorial" is indicative of similarities between water masses in different areas, there can be significant differences in the faunal components (e.g., Indian equatorial versus east Pacific equatorial; east north Pacific central versus west north Pacific central).

Since the distributions of *Argyrolepecus* and *Sternoptyx* are disjunct yet worldwide, a detailed look at the range of each species was made in an attempt to define some of the important distributional parameters. Temperature was considered, as it is often correlated with the distributional limits of fishes. Table 22 represents the temperature range of each species within arbitrarily selected depth limits, corresponding roughly to the depth limits of the species. Tables 20 and 21 illustrate temperature depth profiles from various parts of the ocean where different species occur. As Table 22 illustrates, absolute temperature ranges widely overlap, although certain species tend to be high while others are low. Species occur in colder waters in the Pacific in comparison with the Indian and Atlantic oceans. Dis-

TABLE 20. TEMPERATURE-DEPTH PROFILES FOR VARIOUS PARTS OF THE PACIFIC AND INDIAN OCEANS

Depth (m)	40°N, 150°W <i>Pacific subarctic</i>	34°N, 122°W <i>California</i>	10°N, 120°W <i>Eq Pacific</i>	18°N, 142°W <i>NE Pacific Cent</i>	25°N, 160°E <i>NW Pacific</i>
200	9.5	9	12	13	17
400	6.5	6.5	9.5	8	14
600	5	5	6	6.5	8
800	<5	<5	5.5	5	5
1000	<5	<5	4.5	<5	4.5
Depth (m)	30°S, 85°W <i>SE Pacific Chile</i>	25°S, 130°W <i>SE Pacific</i>	30°S, 160°E <i>SW Pacific</i>	40°S, 140°E <i>Subantarctic</i>	14°S, 115°E <i>Java</i>
200	11	17	21	8.5	14
400	7	11	12	7.5	9
600	6	6.5	9	7	
800	4.5	5.5	7	5	
1000	<5	5	4.5	4.5	
Depth (m)	4°N, 65°E <i>NC Indian</i>	35°S, 65°E <i>SC Indian</i>	35°S, 40°E <i>SW Indian</i>	12°S, 65°E <i>Eq Indian</i>	20°S, 100°E <i>SE Indian</i>
200	14	13	17	15	18
400	11	12	15	10	11
600	10	11	13	7.5	
800	8	9	10	6	
1000	7	6	7	5	
1200	5.5	<5	5	<5	

tributional generalities become more definite, however, upon examination of the horizontal distribution of the various species, coupled with the temperature profiles and general hydrographical characteristics.

The following pattern emerges by com-

paring the various species. *A. gigas* is limited to transitional waters at the boundaries of tropical central or warm water masses and colder temperate waters where roughly the 5° isotherm is deeper than 800 m. *A. affinis* and *A. sladeni* are

TABLE 21. TEMPERATURE-DEPTH PROFILES FOR VARIOUS PARTS OF THE ATLANTIC OCEAN.

Depth (m)	28°N, 87°W <i>N Gulf Mex</i>	24°N, 93°W <i>Gulf Mex</i>	17°N, 60°W <i>Venezuela</i>	16°N, 79°W <i>Caribbean</i>	32°N, 15°W <i>Trop NE Atl</i>	40°N, 20°W <i>N NE Atl</i>	40°N, 50°W <i>NW Atl</i>
200	14	20	15	18	16	13	16
400	9	10	9	11	13	12	12
600	6	8	7	7.5	11	10.5	8
800	5	7	5	6	10	9.5	6
1000	<5	6	<5	5	9	8	<5
1200	<5	5	<5	<5	8	7	<5
	<i>Gulf of Guinea</i>	8°N, 35°W <i>Trop Atl</i>	16°N, 25°W <i>Verdes Isl</i>	16°S, 60°W <i>SW Atl</i>	24°S, 70°W <i>SW Atl</i>	24°S, 5°E <i>SE Atl</i>	
200	14	10	15	20	14	16	
400	9	8	11	10	10	13	
600	6	7	9	6	8	9	
800	<5	6	7	<5	<5	5.5	
1000	<5	5	6	<5	<5	<5	
1200	<5	<5	5.5	<5	<5	<5	

TABLE 22. TEMPERATURE RANGES AT ARBITRARILY CHOSEN DEPTHS FOR THE VARIOUS SPECIES OF ARGYROPELECUS AND STERNOPTYX. FIGURES WERE OBTAINED BY COMPARING HORIZONTAL SPECIES RANGES WITH KNOWN TEMPERATURE-DEPTH PROFILES OVER THIS RANGE.

Species	Depth (m)	Temperature Range (°C)
<i>A. aculeatus</i>	200	15–21 (all oceans)
	400	10–15 (all oceans)
<i>A. olfersi</i>	200	12–13 (all oceans)
	400	9 (Atlantic) 7 (Pacific)
<i>A. lychnus</i>	200	7–12 (Pacific)
	400	6–10 (Pacific)
<i>A. sladeni</i>	200	9–14 (all oceans)
	400	6.5–11 (all oceans)
<i>A. hemigymnus</i>	200	9–18 (all oceans)
	400	6.5–13 (all oceans)
<i>A. affinis</i>	200	9–14 (all oceans)
	400	6.5–11 (all oceans)
<i>A. gigas</i>	400	7–12 (all oceans)
	600	6–10 (all oceans)
<i>S. diaphana</i>	600	5–7 (Pacific); 9–11 (Indian & Atlantic)
	800	5–4.5 (Pacific); 7.5–10 (Indian & Atlantic)
<i>S. obscura</i>	600	7.5–10 (Indian & Pacific)
	800	6–8 (Indian); 4.5–5.5 (Pacific)
	1000	4.5–5 (Indian & Pacific)
<i>S. pseudobscura</i>	800	8–5 (all oceans)
	1000	4–5 (all oceans)

restricted primarily to the eastern boundary currents and areas of upwelling which are characterized by cool water between 300 m and 400 m. *A. olfersi* is restricted to the warmer areas of subpolar waters characterized by 12–13° temperatures at 200 m. *A. hemigymnus* is excluded only from equatorial waters, although biometric data indicates a population structure which corresponds to water mass boundaries. *A. aculeatus* is restricted to warm central water masses in areas bounded approxi-

mately by the 15° isotherm at 200 m. *A. lychnus* occurs only in the Pacific equatorial water mass characterized by cool temperatures between 200 m and 400 m. *S. diaphana* is excluded from the equatorial water masses only. *S. obscura* is limited to equatorial water masses and their boundaries while *S. pseudobscura* is similar to *S. diaphana*, although more restricted to tropical and subtropical waters.

The above distribution pattern is a strong argument for the importance of

TABLE 23. CATCH STATISTICS FOR TWO LARGE SAMPLES OF ARGYROPELECUS FROM THE NORTH ATLANTIC. SIZE CLASS FIGURES REFER TO THE NUMBER OF INDIVIDUALS IN THE SAMPLE WHOSE STANDARD LENGTH FALLS BETWEEN THE SIZE LIMITS; I.E., THERE WERE TWO INDIVIDUALS OF *A. ACULEATUS* WHOSE STANDARD LENGTHS WERE FROM 21 TO 25 MM.

Species	Total Catch	Size Class (mm)									
		10	15	20	25	35	45	55	65	90	90+
<i>A. hemigymnus</i> *	240	9	61	37	43	80	10				
<i>A. aculeatus</i> **	75			3	2	6	13	29	15	8	1

* Atlantis II 13, station 1040, 0940–1125, 320–375 m.

** Chain 32, station 859, 0835–1305, 380 m.

TABLE 24. OCCURRENCE OF THE SPECIES OF *ARGYROPELECUS* AND *STERNOPTYX* IN VARIOUS WATER MASSES. X = TAKEN IN NUMBERS; S = REPORTED IN SMALL NUMBERS USUALLY NEAR WATER MASS BOUNDARIES; O = UNRECORDED; ? = POSSIBLE RECORD.

Water Mass	Species									
	<i>A. gigas</i>	<i>A. affinis</i>	<i>A. hemignathus</i>	<i>A. hyacinthus</i>	<i>A. sladeni</i>	<i>A. aculeatus</i>	<i>A. offersi</i>	<i>S. diaphana</i>	<i>S. obscura</i>	<i>S. pseudobscura</i>
N Atlantic Central	X	X	X	O	X	X	X	X	O	X
S Atlantic Central	X	X	X	O	X	X	S	X	O	X
EN Pacific Central	O	X	X	O	X	O	O	X	O	X
WN Pacific Central	O	O	S	O	O	S	O	X	O	O
ES Pacific Central	S	O	S	O	O	X	S	X	O	X
WS Pacific Central	O	O	S	O	X	X	O	O	O	O
NE Pacific Transitional	O	X	X	X	X	O	O	S	X	O
SE Pacific Transitional	X	X	X	X	X	S	S	X	X	O
Pacific Equatorial	O	S	O	X	O	O	O	S	X	O
Indian Equatorial	S	X	X	O	X	O	O	O	X	S
Indian Central	X	S	X	?	S	X	O	X	S	X
Subantarctic	X	O	X	O	O	O	X	X	O	O
N Pacific Subarctic	O	O	X	O	X	O	O	X	O	O

temperature in defining distributions (e.g., McGowan, 1960; Nafpaktitis, 1968). It is apparent, however, that absolute temperature values per se are not the sole limiting factor and that each water mass can be defined by a host of other physical and biological factors, all of which may be important in limiting distributions.

A number of recent studies indicate that water masses have a biological identity and many widely diverse forms are limited to them (Bieri, 1959; Aron, 1962; Brinton, 1962; McGowan, 1963; Fager and McGowan, 1963). Additional aspects to be considered are the hydrographic features such as boundary areas, transitional waters and upwelling areas which provide further heterogeneity of biological importance. Pelagic hatchetfish distributions are particularly illustrative of the biological similarities of areas with corresponding hydrographic properties. For instance, eastern boundary currents which are quite similar hydrographically (Wooster and Reid, 1963) contain the same hatchetfish species wherever they are found. The same can be said of central gyre areas or subpolar waters.

While the physical and biological properties of the whole water column are important in the ecology of a given water mass, barriers to distribution in hatchetfishes appear to be primarily a function of the environmental properties over the depth range of the species. Furthermore the barriers become less marked with depth so that discontinuities at 800–1000 m occur less often than those from 200–400 m. This is reflected in the broad distributions of the deep living *Sternoptyx* with three closely related species compared to the highly disjunct and more speciose *Argyropelecus* with its more shallow distribution. This same pattern is evident in other deep living forms (David, 1963; Ebeling, 1962; Grice, 1963; Grice and Hulsemann, 1967) where life history features of juveniles or larvae do not complicate the distribution.

Zoogeographic Regions

Several features make the pelagic hatchetfishes particularly well suited to zoogeographical studies. Their distributions are broad, yet limited to waters of similar

TABLE 25. ZOOGEOGRAPHIC REGIONS.

No.	Region	Species Assembly
1.	E Pacific Equatorial	<i>A. lychnus</i> , <i>S. obscura</i> .
2.	N Pacific Transitional	<i>A. affinis</i> , <i>A. hemigymnus</i> , <i>A. sladeni</i> , <i>S. obscura</i> , <i>A. lychnus</i> (<i>S. diaphana</i>).
3.	Pacific Subarctic	<i>A. sladeni</i> , <i>A. hemigymnus</i> (<i>S. diaphana</i>).
4.	EN Pacific Central	<i>A. affinis</i> , <i>A. sladeni</i> , <i>A. hemigymnus</i> , <i>S. diaphana</i> .
5.	WN Pacific Central	<i>A. aculeatus</i> , <i>A. hemigymnus</i> , <i>S. diaphana</i> , <i>S. pseudobscura</i> .
6.	SE Pacific Transitional	<i>A. affinis</i> , <i>A. sladeni</i> , <i>A. hemigymnus</i> , <i>A. lychnus</i> , <i>A. gigas</i> , <i>S. diaphana</i> (<i>A. olfersi</i> , <i>S. obscura</i>).
7.	Pacific Subantarctic	<i>A. olfersi</i> , <i>A. hemigymnus</i> , <i>A. gigas</i> , <i>S. diaphana</i> .
8.	S Pacific Central	<i>A. aculeatus</i> , <i>A. hemigymnus</i> (<i>S. pseudobscura</i>).
9.	Indian Equatorial	<i>A. affinis</i> , <i>A. sladeni</i> , <i>A. hemigymnus</i> , <i>S. obscura</i> .
0.	Java-Indonesian	<i>A. affinis</i> , <i>A. sladeni</i> , <i>A. hemigymnus</i> , <i>S. diaphana</i> , <i>S. obscura</i> .
1.	Indian Central	<i>A. aculeatus</i> , <i>A. hemigymnus</i> , <i>A. gigas</i> , <i>S. diaphana</i> , <i>S. pseudobscura</i> .
2.	Tropical Atlantic	<i>A. sladeni</i> , <i>S. diaphana</i> , <i>S. pseudobscura</i> (<i>A. hemigymnus</i>).
3.	SE Atlantic Transitional	<i>A. affinis</i> , <i>A. sladeni</i> , <i>A. gigas</i> , <i>A. diaphana</i> , <i>S. pseudobscura</i> .
4.	Venezuelan-Caribbean	<i>A. affinis</i> , <i>A. sladeni</i> , <i>A. hemigymnus</i> , <i>S. diaphana</i> , <i>S. pseudobscura</i> , <i>A. aculeatus</i> .
5.	Caribbean-Gulf Central	<i>A. aculeatus</i> , <i>A. hemigymnus</i> , <i>S. diaphana</i> , <i>S. pseudobscura</i> , <i>A. sladeni</i> .
6.	Gulf Peripheral	<i>A. affinis</i> , <i>A. sladeni</i> , <i>A. hemigymnus</i> , <i>A. gigas</i> , <i>S. diaphana</i> .
7.	NW Atlantic Pocket	<i>A. affinis</i> , <i>A. sladeni</i> , <i>S. diaphana</i> , <i>S. pseudobscura</i> .
8.	WN Atlantic Central	<i>A. aculeatus</i> , <i>A. hemigymnus</i> , <i>S. diaphana</i> (<i>A. gigas</i>).
9.	EN Atlantic Central	<i>A. aculeatus</i> , <i>A. hemigymnus</i> , <i>S. diaphana</i> , <i>S. pseudobscura</i> (<i>A. gigas</i>).
0.	NE Atlantic Subarctic	<i>A. olfersi</i> , <i>A. hemigymnus</i> , <i>A. gigas</i> , <i>S. diaphana</i> , <i>S. pseudobscura</i> .
1.	SW Atlantic Central	<i>A. aculeatus</i> , <i>A. hemigymnus</i> , <i>S. diaphana</i> , <i>S. pseudobscura</i> (<i>A. sladeni</i>).
2.	W Mediterranean	<i>A. hemigymnus</i> .
3.	N New Zealand Pocket	<i>A. sladeni</i> .
4.	SE Atlantic Subantarctic	<i>A. olfersi</i> , <i>A. hemigymnus</i> , <i>S. diaphana</i> .

hydrographic properties; they are relatively numerous and easily caught; expatriation is limited; adults and juveniles share the same environment; they are only partial migrators at best and are thus less affected by seasonal fluctuations; and they occur over much of the depth range of the "mesopelagic" environment.

As we have seen above, the water masses

as presently defined are too broad to explain species distributions as we find them. However, the concept of water masses as bodies of water with similar hydrographic and biological properties is important, and seems to be the most significant one in explaining much of the heterogeneity in the midwater environment. The pelagic hatchetfishes are used in Figure 80 as

indicator species of waters of similar properties and their associated discontinuities. The results may add to greater appreciation of water masses—both conceptually and geographically. Table 25 and Figure 80 list the zoogeographic regions and are also an attempt to indicate similarities between regions. The characteristic species assemblages which occur in these regions are listed under the appropriate area. No boundaries were drawn because in most cases they could not be defined. Important isotherms are included and may serve as rough boundaries. Presently defined water mass boundaries (see Sverdrup et al., 1960) in many cases mark the limits of these areas.

Several attempts at defining oceanic zoogeographic regions have been made (Ebeling, 1962; Clarke, 1966) and Figure 80 represents an additional one. No attempt has been made to categorize these regions as primary or secondary, but certainly some regions involve the whole of the mesopelagic environment, while others seem important only at shallower depths. Considerable variation exists in the sharpness of the boundaries and, to some extent, in the degree of species overlap. As knowledge of the oceans and their fauna increases, the nature and extent of these regions and their boundaries will become more apparent.

Areas which are zoogeographic regions and have boundaries which appear throughout the "mesopelagic" environment are the tropical east Pacific, the Indian equatorial region, the northeast Atlantic, and the subantarctic, especially the Pacific portion. There is a wide subtropical belt that is continuous at deeper depths, but is broken into smaller regions above approximately 600 m. The tropical east Pacific has been recognized as a major zoogeographic region, and it seems to have an endemic fauna at all levels (Brinton, 1962; Ebeling, 1962; Johnson and Brinton, 1963). The Indian equatorial region, while not as well known, appears

to be somewhat similar to the equatorial Pacific, at least in some species of hatchetfishes and other fishes as well (Ebeling, 1962; Gibbs and Hurwitz, 1967). The northeast Atlantic is quite different from the western Atlantic in a number of groups (Haffner, 1952; Clarke, 1966; Nafpaktitis, 1968). Additional evidence from this and other studies (Alvarino, 1965; Gibbs, 1968) indicates that the convergence area, especially in the South Pacific, is a major zoogeographical region which may be quite restricted in the South Atlantic and Indian Ocean. The 5° isotherm is much closer to the central water masses at 200 m (Fig. 80), and the distance between the convergences is generally less broad (Sverdrup, 1960).

Regions which are distinctive for the upper 500 m are the warm central water masses of the major gyre systems, and the eastern boundary currents which are cold water areas of transition and upwelling. There are other smaller areas that are important zoogeographically and are faunally similar to the major regions. These include pockets of cold water around the Gulf of Mexico, off South Africa, off the southeast United States (see Haffner on *Chauliodus*, 1952), in the southern Caribbean and tropical Atlantic, off Java, off New Zealand, and southeast of Hawaii.

The Sternoptychidae are represented by a single species in the western Mediterranean, an area which seems distinct from the warmer eastern end. This population is distinct from the North Atlantic one, and this distinction has been documented for other midwater fishes (Marshall, 1963). Hatchetfishes have not been taken in the Red Sea proper (Marshall, 1963) or the Gulf of California (Lavenberg and Fitch, 1966).

Ecological niches and diversity. Speciation pattern, distribution, and population structure are three indicators of diversity, niche breadth, and heterogeneity in the mesopelagic environment. While the worldwide midwater environment is heterogene-

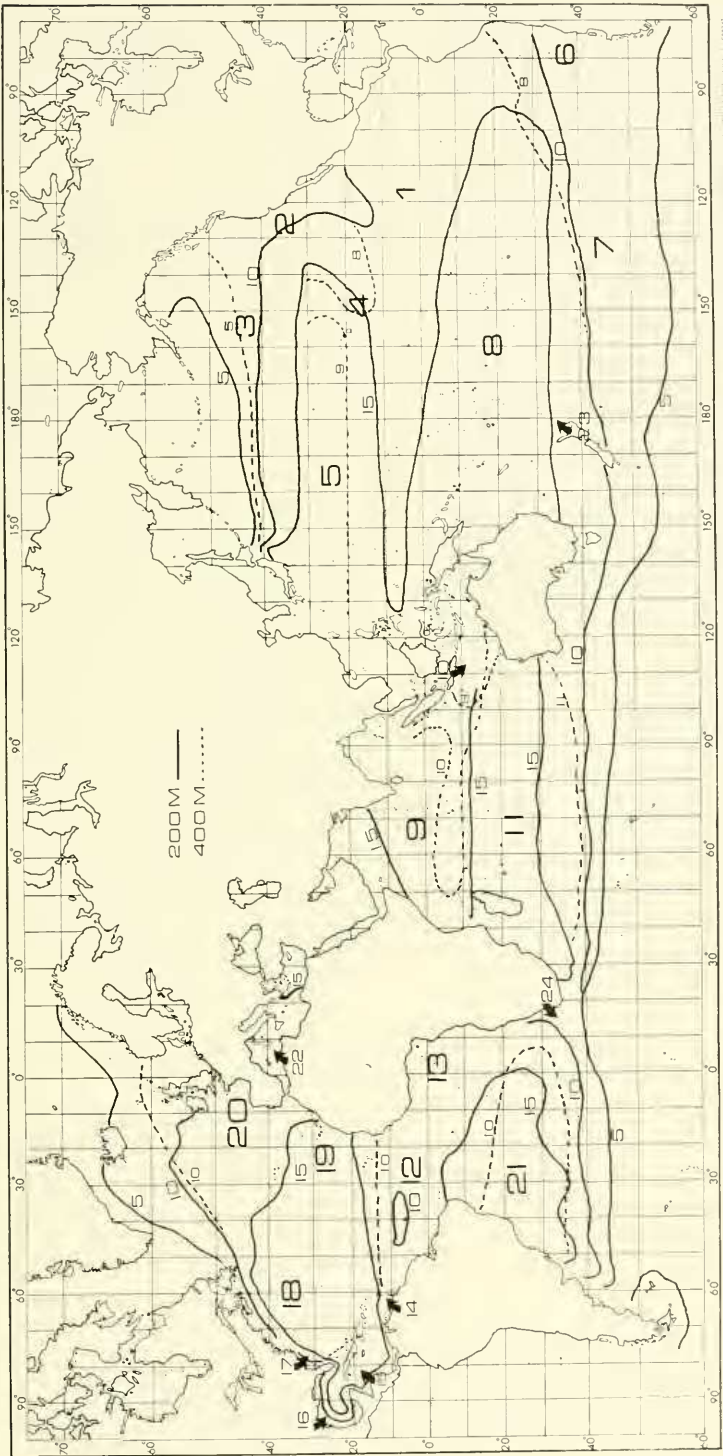


Figure 80. Zoogeographic regions of the mid-depths of the oceans determined from distributions of pelagic hatchetfishes. Solid lines mark isotherms at 200 m; broken lines mark 400 m isotherms. See text and Table 25 for explanation.

ous, it nevertheless appears to be relatively constant, at least in measurable physical parameters, over broad areas. This is reflected in the patterns observed in the three indicators mentioned above.

Measurable niche parameters appear quite broad in hatchetfishes in comparison with freshwater or shore faunas. Overlap between congeneric species is not extensive, and where it does occur there are usually major morphological or vertical distributional differences. Allopatric ranges are the rule. Congeneric coexistence usually requires either a major shift in depth distribution or marked morphological change. Thus *Polyipnus*—often geographically isolated and land associated—is the most speciose genus, while *Sternoptyx*—the deepest living—is the least. There are indications that this broad niche phenomenon occurs in other groups as well (Marshall, 1963).

ACKNOWLEDGMENTS

I wish to acknowledge with appreciation the following sources of support for my study at Harvard University: a two year Aquatic Sciences Fellowship from the Bureau of Commercial Fisheries; travel funds from the United States—Japan Cooperative Program in Science (GF 147) to Harvard University; and assistance from the Harvard Committee on Evolutionary Biology.

My thanks go to the people listed below from numerous institutions whose kind cooperation made this study possible.

- C. Robins, T. Devany, J. Stieger, Institute of Marine Science, University of Miami
- F. Berry, W. Richards, Bureau of Commercial Fisheries, Miami
- R. Lavenberg, Los Angeles County Museum
- J. Savage, J. Paxton, Hancock Foundation, University of Southern California
- K. Suzuki, University of Mie, Japan
- R. Rosenblatt, D. Hoese, Scripps Institute of Oceanography
- E. Ahlstrom, Bureau of Commercial Fisheries, La Jolla
- J. Marr, B. Rothschild, Bureau of Commercial Fisheries, Honolulu
- J. Nielsen, Zoological Museum, Copenhagen
- P. Foxton, J. Badcock, National Institute of Oceanography, England
- P. Greenwood, G. Palmer, British Museum (NH), England
- J. Moreland, Dominion Museum, New Zealand
- D. Cohen, N. Gamblin, L. Schultz, U. S. National Museum, Washington
- B. Zaranuhec, Oceanographic Data Center, Washington

For their understanding discussions and for such gracious hospitality, I am particularly grateful to T. Abe of the University of Tokyo, and to E. Bertelsen of the Danish Carlsberg Foundation.

I wish to thank the staff of the Woods Hole Oceanographic Institute, especially Richard Backus and James Craddock, who offered me every encouragement and gave freely of their time and facilities.

My thanks also to Jules Crane of Cerritos College, who kindly provided fossils from his collection; to Stanley Weitzman of the U. S. National Museum for his thoughts and ideas on the subject of osteology; and to W. Bossert of Harvard University, who introduced me to the world of computer science.

I wish to acknowledge the staff of the Museum of Comparative Zoology, particularly Myvanwy Dick; the graduate students of the fish department whose assistance and discussion were invaluable; B. Nafpaktitis and M. Eckardt of the University of Southern California; Sharon Horn, and Nancy Smith (illustrations); M. Howbert, who provided many of the original illustrations through the courtesy of the Woods Hole Oceanographic Institute; K. S. Baird, and Penelope Lasnik for her many hours before the editorial mast.

Finally, I owe a special debt of gratitude and thanks to Giles W. Mead, my major

professor, for his guidance, encouragement, criticism, and support in making my graduate years at Harvard a full and rich experience.

SUMMARY

1. The Sternoptychidae are primitive stomiatoïd fishes closely related to the Gonostomatidae, but different from them morphologically; most of this difference is related to the peculiar deep body shape of the former.
2. The Sternoptychidae probably arose during the early Tertiary as part of an early stomiatoïd radiation. Miocene fossils of *Argyropelecus* could not be distinguished from their modern counterparts, indicating little osteological evolution in this genus since then.
3. The three genera in the family are widely divergent; each has specialized in a separate direction.
4. *Polyipnus* occurs only in close association with land. Its pattern of distribution and speciation closely parallels that of many tropical shore species.
5. *Argyropelecus* is distributed widely in all tropical and temperate seas. It is a partial migrator not often entering the upper 100 m at night. Adults and juveniles are found in about the same depth range. *Argyropelecus* inhabits the upper "mesopelagic" zone (100–600 m).
6. *Sternoptyx* is distributed horizontally within the same limits as *Argyropelecus*. It inhabits the lower "mesopelagic" zone (500–1500 m) and does not appear to migrate diurnally.
7. *Argyropelecus* and *Sternoptyx* species are restricted in distribution, each species seemingly restricted to waters with similar hydrographic and biological properties.
8. *Argyropelecus* is more speciose and shows more morphological variation than *Sternoptyx*. Species ranges in *Sternoptyx* are much broader, indicating that barriers to distribution and heterogeneity may be more pronounced in the upper "mesopelagic" than in the lower.
9. Certain species assemblages occur in waters which are hydrographically similar. These assemblages are used to zoogeographically define distinct areas of the world's oceans.
10. Ecological niches in the Sternoptychidae are broad over measurable niche parameters. Allopatric species ranges are the rule and, where congeneric sympatric species occur, there is usually a considerable amount of morphological or vertical distinctness.

APPENDIX A

INSTITUTIONS AND CRUISES FROM WHICH MATERIAL WAS EXAMINED OR RECORDED

1. Institutions and their abbreviations.

Collections of T. Abe and O. Suzuki, Tokyo, Japan.	ABE
Australian Museum, Sidney, Australia.	AM
Bureau of Commercial Fisheries, Honolulu, Hawaii.	BCFH
Bureau of Commercial Fisheries, La Jolla, California.	BCFL
Bureau of Commercial Fisheries, Miami, Florida.	BCFM
British Museum (Natural History), London, England.	BMNH
Dominion Museum, Wellington, New Zealand.	DMNZ
International Indian Ocean Expedition.	IOE
Biologische Anstalt Helgoland (Meteor Indian Ocean Expedition), Hamburg, Germany.	IOES
Los Angeles County Museum, Los Angeles, California.	LACM
Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.	MCZ

APPENDIX A (Continued)

Musée National d'Histoire Naturelle, Paris, France.	MNHNP
Musée Royale d'Afrique Central, Tervuren.	MRAC
National Institute of Oceanography, Surrey, England.	NIO
Oceanographic Data Center, Washington, D.C.	ODC
Scripps Institute of Oceanography, La Jolla, California.	SIO
Institute of Marine Science, University of Miami, Florida.	UMML
John Hancock Foundation, University of Southern California, Los Angeles, California.	USC
U.S. National Museum, Washington, D.C.	USNM
Woods Hole Oceanographic Institute, Woods Hole, Massachusetts.	WHOI
Zoological Museum, Copenhagen, Denmark.	ZMUC

2. Institutions and Cruises from Which Material Was Examined and Recorded.

Institution	Ship and Cruise	Location
ABE	local fishing vessels	Japan
AM	holotypes only	Australia
BCFH	HUGH M. SMITH 30	C Pacific
	HUGH M. SMITH 31	C Pacific
BCFL	larval and juveniles only	EN Pacific
BCFM	GERONIMO	Tropical Atlantic
	SILVER BAY	Florida, Gulf of Mexico
	OREGON	Gulf of Mexico
BMNH	DISCOVERY and others	Worldwide
DMNZ	TUI	New Zealand
HOE	ANTON BRUUN 3 and 6	Indian Ocean
IOES	METEOR (holotype description)	Indian Ocean
LACM	VELERO	NE Pacific
MCZ	ATLANTIS, CAPTAIN BILL III	N Atlantic
	GOSNOLD, BRUUN 13,	Chile, Tropical Atlantic
	CHAIN 17-49, miscellaneous collections	Mediterranean
MNHNP	holotypes only	Atlantic
MRAC	holotype	W African Coast
NIO	DISCOVERY (1955-1965)	NE Atlantic, Indian Ocean
ODC	USNS GILLISS	N Atlantic, Caribbean
SIO	COBB 208, 303	NE Pacific
	BLACK DOUGLASS 203, 303	NE Pacific
	HORIZON	N Pacific
	HOLIDAY, TETHYS	C & S Pacific
	MONSOON, BAIRD	C & S Pacific
UMML	GERDA	Florida, Gulf of Mexico
	PILLSBURY	Caribbean, Gulf of Guinea
USC	USNS ELTANNIN	Subantarctic, Pacific
USNM	ALBATROSS, OREGON	Atlantic, Pacific
	SILVER BAY, COMBAT	
WHOI	CHAIN 60, 72, ATLANTIS II 13	Caribbean, Gulf of Mexico
	ATLANTIS II 31	N & SW Atlantic
ZMUC	GALATHEA	World Cruise
	THOR and miscellaneous collections	N Atlantic, Mediterranean

APPENDIX B (Continued)

Argyroleucus hemigymnus (Form A)

Night

Depth	0	5	Catch		50	100	100+	N
			10	20				
100	20	1	0	0	0	0	0	1
200	9	1	0	0	0	0	0	1
300	11	0	0	0	0	0	0	0
400	2	0	0	0	0	0	0	0
500	4	0	0	0	1	0	0	1
600	0	0	0	0	0	0	0	0
700	3	0	0	0	0	0	0	0
1000	3	0	0	0	0	0	0	0
2000	2	0	0	0	0	0	0	0
2001+	0	0	0	0	0	0	0	0

Caribbean and Gulf of Mexico

Depth	0	5	Catch		50	100	100+	N
			10	20				
100	23	7	1	1	0	0	0	9
200	29	0	0	2	0	0	0	2
300	20	0	0	0	0	2	0	2
400	8	1	1	0	2	0	0	4
500	23	0	1	1	0	0	0	2
600	14	0	0	0	0	0	0	0
700	5	3	1	0	0	0	0	4
1000	22	1	0	0	0	0	0	1
2000	5	0	0	0	0	0	0	0
2001+	0	0	0	0	0	0	0	0

North Atlantic (see Day)

Depth	0	5	Catch		50	100	100+	N
			10	20				
100	5	0	0	0	0	0	0	0
200	3	0	0	0	0	0	0	0
300	4	1	0	0	0	0	0	1
400	16	2	1	1	1	0	0	5
500	3	0	0	1	0	0	0	1
600	2	0	0	0	0	0	0	0
700	5	2	0	0	0	0	0	2
1000	8	2	1	0	0	0	0	3
2000	11	2	2	0	0	0	0	4
2001+	6	1	1	0	0	0	0	2

Southern Ocean (Pacific)

Depth	0	5	Catch		50	100	100+	N
			10	20				
100	35	2	0	0	0	0	0	2
200	7	0	0	0	0	0	0	0
300	7	7	2	0	1	0	0	10
400	0	0	0	0	0	0	0	0
500	7	0	0	0	0	0	0	0
600	0	0	0	0	0	0	0	0
700	0	0	0	0	0	0	0	0
1000	0	0	0	0	0	0	0	0
2000	3	1	0	0	0	0	0	1
2001+	0	0	0	0	0	0	0	0

Pacific (California)

Argyroleucus hemigymnus (Form A)

Day

Depth	0	5	Catch		50	100	100+	N
			10	20				
100	2	0	1	0	0	0	0	1
200	8	0	0	0	0	1	0	1
300	10	0	0	1	1	0	0	2
400	12	3	1	2	2	0	2	10
500	15	7	3	4	3	3	1	21
600	10	2	1	3	2	1	0	9
700	4	0	0	0	2	1	0	3
1000	25	5	0	1	0	0	0	3
2000	6	0	1	0	0	0	0	1
2001+	0	0	0	0	0	0	0	0

North Atlantic (20°-40°N, 5°-70°W)

Depth	0	5	Catch		50	100	100+	N
			10	20				
100	1	0	0	0	0	0	0	0
200	0	0	0	0	0	0	0	0
300	2	1	0	2	0	0	0	3
400	11	3	3	3	0	0	0	9
500	4	3	1	1	1	0	0	6
600	2	1	0	0	1	0	0	1
700	3	1	0	0	0	0	0	1
1000	6	1	0	0	0	0	0	0
2000	10	0	0	0	0	0	0	0
2001+	1	0	0	0	0	0	0	0

Gulf of Mexico, Caribbean

Depth	0	5	Catch		50	100	100+	N
			10	20				
100	0	1	0	0	0	0	0	1
200	1	1	0	0	0	0	0	1
300	3	1	0	0	0	0	0	1
400	0	3	0	0	0	0	0	3
500	0	2	0	0	0	0	0	2
600	1	1	0	0	0	1	0	2
700	0	1	0	0	0	0	0	1
1000	2	4	2	1	1	0	0	8
2000	4	6	1	0	1	0	0	8
2001+	3	3	0	0	0	0	0	3

Southern Ocean (Pacific)

Depth	0	5	Catch		50	100	100+	N
			10	20				
100	8	0	0	0	0	0	0	0
200	8	0	0	0	0	0	0	0
300	11	1	0	1	0	0	0	2
400	4	0	1	0	0	0	0	1
500	3	2	1	0	0	0	0	3
600	1	0	0	0	0	0	0	0
700	1	2	0	0	0	0	0	2
1000	0	0	0	0	0	0	0	0
2000	3	7	0	0	0	0	0	7
2001+	0	1	0	0	0	0	0	1

Pacific (California)

APPENDIX B (Continued)

Argyropelecus hemigymnus (Form B)

									Night									
Depth	0	5	Catch 10	20	50	100	100+	N	Depth	0	5	Catch 10	20	50	100	100+	N	
100	21	0	0	0	0	0	0	0	100	27	3	1	0	1	0	0	5	
200	10	0	0	0	0	0	0	0	200	21	6	2	2	0	0	0	4	
300	9	2	0	0	0	0	0	2	300	17	1	0	0	2	0	0	2	
400	2	0	0	0	0	0	0	0	400	7	1	2	0	0	1	0	4	
500	3	2	0	0	0	0	0	2	500	2	1	1	1	0	0	0	3	
600	0	0	0	0	0	0	0	0	600	0	2	4	0	1	0	0	5	
700	3	0	0	0	0	0	0	0	700	4	0	1	0	0	0	0	1	
1000	3	0	0	0	0	0	0	0	1000	14	2	0	3	1	0	0	6	
2000	2	0	0	0	0	0	0	0	2000	1	0	1	0	0	0	0	1	
2001+	0	0	0	0	0	0	0	0	2001+	0	0	0	0	0	0	0	0	
Gulf of Mexico, Caribbean									North Atlantic (see Day)									

Argyropelecus hemigymnus (Form B)

Day									Night								
Depth	0	5	Catch 10	20	50	100	100+	N	Depth	0	5	Catch 10	20	50	100	100+	N
100	4	0	0	0	0	0	0	0	100	1	0	0	0	0	0	0	0
200	10	0	0	0	0	0	0	0	200	2	0	0	0	0	0	0	0
300	14	0	0	0	0	0	0	0	300	3	1	0	0	0	0	0	1
400	22	0	0	0	0	0	1	1	400	3	0	0	0	0	0	0	0
500	31	1	1	0	0	0	0	1	500	2	0	0	0	0	0	0	0
600	14	3	3	0	0	0	0	6	600	2	0	0	0	0	1	0	1
700	11	0	0	1	0	0	0	1	700	1	0	0	0	0	0	0	0
1000	29	1	0	0	0	0	0	1	1000	9	1	0	0	0	0	0	1
2000	7	0	0	0	0	0	0	0	2000	10	2	0	0	0	0	0	2
2001+	0	0	0	0	0	0	0	0	2001+	6	0	0	0	0	0	0	0
N Atlantic (20°-40°N, 5°-70°W)									Southern Ocean (Pacific)								

Depth	Catch							
	0	5	10	20	50	100	100+	N
100	1	0	0	0	0	0	0	0
200	0	0	0	0	0	0	0	0
300	5	0	0	0	0	0	0	0
400	20	0	0	0	0	0	0	0
500	10	0	0	0	0	0	0	0
600	3	1	0	0	0	0	0	1
700	4	0	0	0	0	0	0	0
1000	7	0	0	0	0	0	0	0
2000	10	0	0	0	0	0	0	0
2001+	1	0	0	0	0	0	0	0

Gulf of Mexico, Caribbean

APPENDIX B (Continued)

Argyrolepecus aculeatus
Night

Depth	Catch							
	0	5	10	20	50	100	100+	N
100	25	4	2	1	0	0	0	7
200	18	10	2	0	1	0	0	13
300	21	0	1	0	0	0	0	1
400	8	3	1	0	0	0	0	4
500	17	7	1	0	0	0	0	8
600	8	6	0	0	0	0	0	6
700	0	7	2	0	0	0	0	9
1000	20	3	0	0	0	0	0	3
2000	5	0	0	0	0	0	0	0
2001+	0	0	0	0	0	0	0	0

North Atlantic

Depth	Catch							
	0	5	10	20	50	100	100+	N
100	8	6	1	0	2	0	0	9
200	0	3	3	1	1	2	0	10
300	5	3	0	2	0	0	0	5
400	0	0	0	0	0	0	0	0
500	2	1	0	0	0	0	0	1
600	0	0	0	0	0	0	0	0
700	2	0	0	0	0	0	0	0
1000	2	1	0	0	0	0	0	1
2000	0	0	0	0	0	0	0	0
2001+	0	0	0	0	0	0	0	0

Gulf of Mexico, Caribbean

Day

Depth	Catch							
	0	5	10	20	50	100	100+	N
100	4	0	0	0	0	0	0	0
200	7	2	1	0	0	0	0	3
300	9	5	0	0	0	0	0	5
400	6	8	4	0	4	1	0	17
500	10	17	1	4	2	0	0	24
600	10	8	0	0	2	0	0	10
700	9	4	0	0	0	0	0	4
1000	24	6	0	1	0	0	0	7
2000	6	0	0	1	0	0	0	1
2001+	0	0	0	0	0	0	0	0

North Atlantic (20°-40°N; 5°-70°W)

Depth	Catch							
	0	5	10	20	50	100	100+	N
100	0	0	0	0	0	0	0	0
200	0	0	0	0	0	0	0	0
300	0	3	1	0	0	0	0	4
400	4	3	2	0	7	0	0	12
500	3	3	0	1	2	0	0	6
600	1	1	0	0	0	0	0	1
700	1	0	0	0	0	0	0	0
1000	2	1	0	0	0	0	0	1
2000	4	0	0	0	0	0	0	0
2001+	0	0	0	0	0	0	0	0

Gulf of Mexico, Caribbean

Argyrolepecus olfersi

Depth	Night Catch							
	0	5	10	20	50	100	100+	N
100	34	1	0	0	0	0	0	1
200	23	4	2	0	0	0	0	6
300	21	2	1	0	0	0	0	3
400	22	6	0	0	0	0	0	6
500	21	2	1	0	0	0	0	1
600	7	2	0	0	0	0	0	2
700	4	0	0	0	0	0	0	0
1000	24	1	0	0	0	0	0	1
2000	17	1	0	0	0	0	0	1
2001+	0	0	0	0	0	0	0	0

Atlantic and Southern Ocean

Depth	Day Catch							
	0	5	10	20	50	100	100+	N
100	4	0	0	0	0	0	0	0
200	8	0	1	0	0	0	0	1
300	13	1	0	0	0	0	0	1
400	20	2	0	0	0	0	0	2
500	26	1	0	0	0	0	0	1
600	13	0	1	0	0	0	0	1
700	9	0	0	0	0	0	0	0
1000	26	3	0	0	0	0	0	3
2000	13	4	0	0	0	0	0	4
2001+	0	0	0	0	0	0	0	0

Atlantic and Southern Ocean

Argyrolepecus sladeni

Depth	Night							
	0	5	10	20	50	100	100+	N
100	19	1	0	1	0	0	0	2
200	10	0	0	0	0	0	0	0
300	3	5	1	1	0	0	0	7
400	0	1	0	0	0	0	0	1
500	3	2	0	0	0	0	0	2
600	0	0	0	0	0	0	0	0
700	2	1	0	0	0	0	0	1
1000	3	0	0	0	0	0	0	1
2000	0	2	0	0	0	0	0	2
2001+	0	0	0	0	0	0	0	0

Gulf of Mexico, Caribbean, Gulf of Guinea

Depth	Night							
	0	5	10	20	50	100	100+	N
100	35	3	0	0	0	0	0	3
200	6	1	2	0	0	0	0	3
300	7	10	2	0	0	0	0	12
400	13	6	1	0	1	0	0	8
500	7	4	0	0	0	0	0	4
600	2	0	0	0	0	0	0	0
700	7	0	0	0	0	0	0	0
1000	11	0	0	0	0	0	0	0
2000	2	2	0	0	0	0	0	2
2001+	0	0	0	0	0	0	0	0

Pacific (California)

Day

Gulf of Mexico, Caribbean, Gulf of Guinea

Argyropelecus lychnus

California, Chile, Tropical Pacific

Sternoptyx obscura

Indian Ocean

Sternoptyx pseudobscura

Indian Ocean

APPENDIX B (Continued)

Depth	Catch							
	0	5	10	20	50	100	100+	N
100	2	1	1	0	0	0	0	2
200	0	0	0	0	0	0	0	0
300	0	1	0	0	0	0	0	1
400	0	2	0	0	0	0	0	2
500	0	2	0	0	0	0	0	2
600	0	0	0	0	0	0	0	0
700	0	0	0	0	0	1	0	1
1000	0	0	0	0	0	0	0	0
2000	0	0	0	1	1	0	0	2
2001+	0	0	0	0	0	0	0	0

Gulf of Guinea

Depth	Catch							
	0	5	10	20	50	100	100+	N
100	15	1	0	0	0	1	0	2
200	10	0	0	0	0	0	0	0
300	4	3	3	0	0	0	0	6
400	0	0	0	0	0	0	0	0
500	2	1	0	0	0	0	0	1
600	0	0	0	0	0	0	0	0
700	1	0	0	0	1	0	0	1
1000	0	2	0	1	0	0	0	3
2000	0	0	0	0	0	0	0	0
2001+	0	0	0	0	0	0	0	0

Gulf of Mexico and Caribbean

Sternoptyx diaphana

Night

Depth	Catch							
	0	5	10	20	50	100	100+	N
100	0	0	0	0	0	0	0	0
200	8	2	0	0	0	0	0	2
300	0	0	0	0	0	0	0	0
400	4	1	0	0	0	0	0	1
500	3	0	0	0	0	0	0	0
600	6	0	0	0	0	0	0	0
700	5	1	0	0	0	0	0	1
1000	8	2	1	0	0	0	0	3
2000	3	2	0	0	0	0	0	2
2001+	0	0	0	0	0	0	0	0

Western Indian Ocean

Depth	Catch							
	0	5	10	20	50	100	100+	N
100	30	0	0	0	0	0	0	0
200	26	0	0	0	0	0	0	0
300	19	0	0	0	0	0	0	0
400	6	1	0	0	0	0	0	1
500	18	2	0	0	0	0	0	2
600	5	3	0	0	1	0	0	4
700	0	2	0	1	1	0	0	4
1000	7	1	1	2	3	0	0	7
2000	2	0	0	1	0	0	0	1
2001+	0	0	0	0	0	0	0	0

North Atlantic (30°–45°N, 20°–70°W)

Day

Depth	Catch							
	0	5	10	20	50	100	100+	N
100	1	0	0	0	0	0	0	0
200	3	0	0	0	0	0	0	0
300	3	1	0	0	0	0	0	1
400	4	0	0	0	0	0	0	0
500	7	2	0	0	0	0	0	2
600	3	2	2	2	0	0	0	6
700	2	1	0	1	1	0	0	3
1000	2	3	2	4	1	0	0	10
2000	0	0	1	0	1	0	0	2
2001+	0	0	0	0	0	0	0	0

NE Atlantic

Depth	Catch							
	0	5	10	20	50	100	100+	N
100	1	0	0	0	0	0	0	0
200	2	0	0	0	0	0	0	0
300	3	0	0	0	0	0	0	0
400	1	0	0	0	0	0	0	0
500	2	0	0	0	0	0	0	0
600	2	0	0	0	0	0	0	0
700	0	0	0	0	0	0	0	0
1000	3	1	0	1	1	0	0	3
2000	3	3	0	1	3	0	0	7
2001+	0	1	0	0	0	0	0	1

Southern Ocean (Pacific)

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